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THE ORIGIN OF SPECIES, V: SPECIATION AND MUTATION

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AROUSED by the late William H. Bateson's statements in his South African and Toronto addresses to the effect that we know neither the *modes* nor the *causes* of the origin of species, the writer opened in 1925 a series of papers, enumerated below (I–V), of which the present is the final one, ranking as No. V in the series:

THE ORIGIN OF SPECIES AS REVEALED BY VERTEBRATE PALEONTOLOGY (I). Address delivered before National Academy of Sciences, April 28, 1925, and published in *Nature*, June 13 and 20.

THE ORIGIN OF SPECIES, II: DISTINCTIONS BETWEEN RECTIGRADATIONS AND ALLOMETRONS. Read before National Academy of Sciences, November 11, 1925, and published in its *Proceedings*, Vol. 11, No. 12.

THE ORIGIN OF SPECIES, 1859–1925 (III). Read at dedication of new Yale Museum, December 29, 1925, and published in its Bulletin I, Number 1.

THE PROBLEM OF THE ORIGIN OF SPECIES AS IT APPEARED TO DARWIN IN 1859 AND AS IT APPEARS TO US TO-DAY (IV). Read before Section D (Zoology) of the British Association at Oxford, August 5, 1926, and published in *Nature*, August 21, 1926. Republished with corrections in *Science*, October 8, 1926.

THE ORIGIN OF SPECIES, V: SPECIATION AND MUTATION.

Renewed support of the exclusive origin of species by *mutation* with lack of proof of environmental influence has recently been given by Crampton (1925, p. 35), by Calkins (1926, p. 350) and by Morgan (1926, p. 106), who says:

Darwin rested his case for evolution on the observed small differences that all animals and plants show. Now, while we realize to-day that many of these slight differences are not inherited, we also know that amongst them

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there are some that are inherited and that these, so far as we know, have arisen as mutations. At present there is no evidence that will stand the test of criticism in favor of any other origin than that all known variations owe their appearance to the same process of mutation that also produces the larger differences; and, I repeat, that there is much explicit evidence to show that very small differences, that add to or subtract from characters already present, do appear by mutation.

The present paper (V) presents in more detail the zoological data on which the fourth paper of the series was based, including a fairly complete bibliography of the papers referred to. The writer is again indebted to his colleagues in the American Museum for their more careful scrutiny of the facts and figures in their previous statements; to R. I. Pocock for his note on the zebras; to W. H. Osgood and F. B. Sumner for revision of their previous statements.

The present paper is divided as follows:

(1) 1859–1926. Discovery and naming of Subspecies and Geographic Varieties.

(2) Authority for the Word "Speciation."

(3) Principles of Continuous Geographic Isolation, Intergradation and Speciation in the genus Io.

(4) 1859–1926. Discoveries relating to the Origin of Species in Fishes.

(5) Discoveries relating to the Origin of Species in Amphibia and in Reptilia; (a) Intergrades in Amphibia; (b) Intergrades in Reptilia.

(6) 1859–1926. Discoveries relating to the Origin of Species, Subspecies and Mutations in Birds; (a) Species-origin environmental and mutational in birds; (b) Stresemann on Mutations; (c) Chapman on Zonal Speciation; (d) Speciation and Mutation of the South American House Wren.

(7) 1859–1926. Discoveries relating to the Origin of Species in Mammals; (a) Speciation of the Deer Family around the World on the Northern Parallels; (b) Probable Intergradation in Zebras and Foxes; (c) Speciation of the Deer-mice in Contiguous North American Areas; (d) Isolation in the Origin of Localized Races of *Peromyscus* and of *Thomomys*; (e) Speciation in the Gopher (*Thomomys*).

(8) Summary of Speciation and Mutation as observed in the Living Vertebrates.

1859–1926. Discovery and Naming of Subspecies and Geographic Varieties

In Darwin's own library in the Botany School at Cambridge we find some volumes which cover the mammalogy of his day; for example, Lesson's "Manuel de Mammal-

ogie'' (1827), in which 1,124 fossil and living species are listed by number, and Agassiz' ''Nomenclatoris Zoologici Index Universalis'' (1848), in which 889 genera of mammals are listed. Also accessible to Darwin were the complete works of Linnaeus, Buffon, Bonaparte, Audubon and other great zoologists. Darwin was little concerned about the *number* of species known in his day; he remarked that *transitions between species and varieties* are rare and he would have been the first to welcome the numerous transitions now observable among fishes, reptiles, birds and mammals. Remember we are here speaking only of the period 1837–1859, when ''The Origin'' was being written, not of the subsequent period of ardent exploration.

Vertebrates. Günther and Shipley list the number of vertebrate species known in the years 1830 to 1881 and 1924 as below. The lists of Sharpe, Chapman and Anthony include species and subspecies.

	1837–1859	1881–1886	1924	1926	1909	1926
	Lesson-Agassiz Darwin	Günther-Leunis Shipley	Poole and others	American Museum Anthony	Sharpe	Chapman Estimated
Mammals	1,200	2,300	12,540	13,000		
Birds	3,600	11,000	16,000		18,939	24,000
Reptiles and Amphibians	543	3,400	9,000			
Fishes	3,500	11,000	20,000			

Mammals. Several authorities, including Sherborn, the conservative historiographer of species, agree that not more than 1,200 species of mammals were known when Darwin was writing ''The Origin of Species''; the increase to the present day is over tenfold, and the present number is being rapidly expanded through explorations in Asia, Africa and South America. The present

estimated total of 13,000 living species and subspecies of mammals is geographically subdivided as follows:

Asia. Estimated after Allen and Anthony	Europe. Estimated after Miller, 1912, and subsequent discovery	Africa. Estimated after Herbert Lang	Australia. Estimated after H. C. Raven	N. America. Estimated after Miller, 1924, and subsequent discovery	S. America. Estimated after Anthony
3,550	1,000	1,000–2,000	350	2,600	3,500

To summarize and contrast successive lists, the estimates of mammals are approximately as follows:

1827	Lesson: Living and fossil species	1,124
1924	Poole: Living species and subspecies	12,540

Accordingly, tenfold is a conservative estimate of the increase of our knowledge of mammals alone since Darwin's volume of 1859, but the enumeration is not on equal terms, because we include not only species but numberless subspecies listed in trinomials and still largely regarded as geographical variations. It has, however, recently been shown by experiment (Sumner, 1924, III) that many, if not all, subspecies *are stable under changed conditions of environment.* Consequently, while under suspicion as to reality, often vexatious and inconvenient, and always annoying to the systematist, *well-authenticated subspecies are of priceless value to the biologist who seeks to ascertain the conditions under which new species arise.* In fact, many true "subspecies" and "geographic variations" are now known to be germinal transitions, intermediates and intergradations from "Species" to "Species" of the higher kind known to Darwin.

AUTHORITY FOR THE WORD "SPECIATION"

In the classic shades of Oxford the writer hesitated to introduce the etymologically doubtful word "speciation" now being quite widely used in less classic America. On

this linguistic point (1) D'Arcy Thompson, the eminent zoological classicist of St. Andrews, writes, July 16, 1926:

Speciation will really not do for "the making of species." Obviously the word is, or ought to have been, *specification*, but that has long ago taken unto itself a different meaning. *Speciation* is not Latin; it is, however, *understandable*. You are therefore on the horns of a dilemma, as it seems to me: you may throw conservative scholarship to the winds and, heading straight for practical utility, talk of speciation as much as you please; or, alternately, you must be content with plain English and talk of the *making*, or the *origin*, of species, or any similar descriptive phrase. I feel pretty sure that, speaking in Oxford, the atmosphere of the place will exercise its conservative influence on you.

(2) L. Davies Sherborn, July 20, 1926, advises:

The word "speciation" has no English usage. I suppose it might be derived from *speciatus-a-um*. John Evelyn, 1664, in Sylva, p. 1679, uses "specify" for breaking into species—hence "specification" (now used in another sense) but this has priority over your "speciation."

In a second communication, however, Dr. Sherborn writes as follows:

The word is justified, but ugly. We can only suggest "differentiation into species," more clumsy but more precise and in accordance with the English language, which is inelastic as compared with many others. "Speciation" has already received two meanings (as below) but the first example seems to be the use you want: "Speciation and Host Relationships of Parasites," (Chandler, 1923. *Journ. Parasitol.*, XV, 3, p. 326). "Speciation" here seems to be used in the sense of the formation or evolution of species. "Speciation and Specificity in the Nematode genus Strongyloides," (Sandground, 1925. *Journ. Parasitol.*, XII, 2, p. 59). Here "speciation" appears to be used in the sense of "systematic differentiation between species" (*i.e.*, in the mind of the systematist). "Specificity" appears to mean adaptation to particular hosts.

(3) P. Chalmers Mitchell, secretary of the Zoological Society of London, referring to previous American usage, writes, July 25, 1926:

"Speciation" says what you wish to say; the word is required; the word is already used in America in the sense you propose. There are rough analogies: variation and varieties, glaciation and glaciers. Language is dynamic, etymology is static. Therefore use "speciation."

Principles of Continuous Geographic Isolation, Intergradation and Speciation in the Genus Io[2]

A striking parallel to the subspeciation of *Troglodytes* and *Peromyscus* is seen in the fresh-water gastropod

[2] Willard G. Van Name: Notes supplied for this paper, 1926.

genus *Io* of the family Pleuroceridae observed by Adams[3] in the Tennessee River and its branches, where it is con-

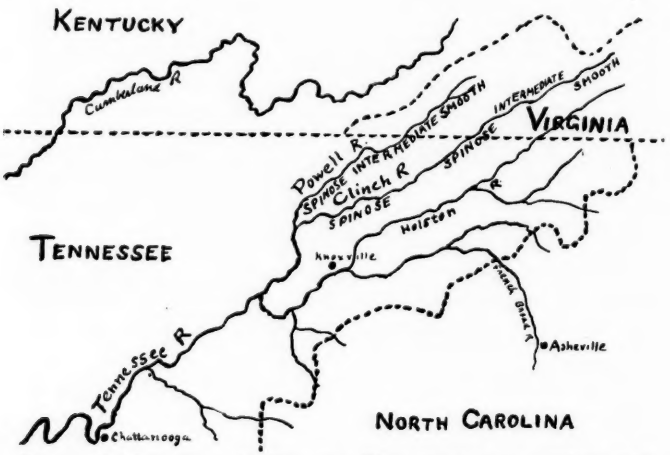


FIG. 1. Headwaters of the Tennessee River, showing the northern tributaries, the Powell and the Clinch, from which Adams collected subspecies of the fresh-water gastropod genus *Io*.

fined, chiefly above Chattanooga (Fig. 1). In two of the main branches, the Powell River and the Clinch River, as we proceed upstream from outlet to source, we pass from the extremely spinose, C, through the sub-spinose, B, into the smooth, A, condition (Fig. 2) without interruption (*i.e.*, by intergradation). In headwaters of both these rivers the shells are smooth or nearly so; as we proceed downstream from source to outlet the shells gradually intergrade from smooth to spinose, first through the development of conical tubercles, which in shells from the lower reaches of the river become strong conical spines. Collections of smooth specimens from the headwaters are quite uniform and are totally unlike collections of spinose specimens from the lower parts of the streams, which are also quite uniform. At intermediate points

[3] C. C. Adams: "Variation in *Io*." *Proc. Amer. Assoc. Adv. Sci.* 1900, pp. 208–225, Pls. I–XXVII.

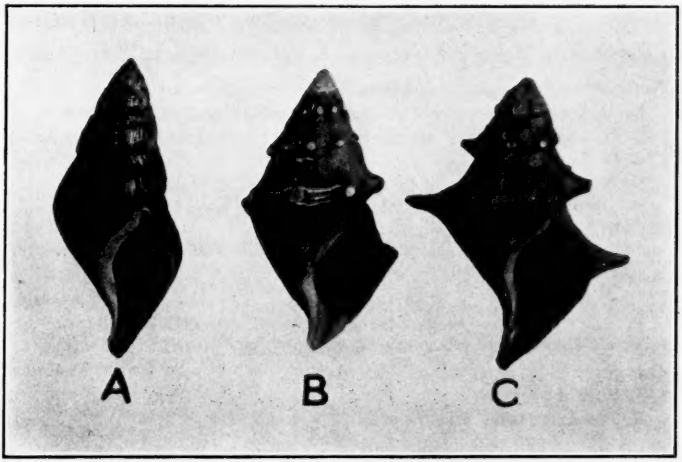


FIG. 2. Intergradation of shells in the genus *Io* of the family Pleuroceridae; collected in the Powell and Clinch rivers (C. C. Adams, *Proc. Amer. Assoc. Adv. Sci.*, 1900, pp. 208–225). A, smooth intergrades at the river source; B, sub-spinose intergrades in midstream; C, extremely spinose intergrades downstream, near outlet.

along the streams specimens intermediate in character prevail with some admixture of smoother and more spiny individuals; so complete is the intergradation that Adams considers them all one species, *Io fluvialis* (Say), 1825, though several species had been recognized by most authors.

Conclusion, Adams, 1900. The want of complete geographic isolation between A, smooth, and C, spinose, obviously prevents a division of the genus *Io* into a smooth species A and an extremely spinose species C.

1859–1926. DISCOVERIES RELATING TO THE ORIGIN OF SPECIES IN FISHES

The outstanding ichthyologists whose writings bear on our problem are arranged by the continents in which their chief observations have been made. The list includes recent systematists and classifiers of fishes, as well as those who have especially directed our attention to the

matter of geographic variation and speciation (names prefixed with a star):

North America:
E. D. Cope
T. N. Gill
*C. L. Hubbs
*D. S. Jordan
B. Dean } fossil
C. R. Eastman } fishes

Asia:
*L. S. Berg
F. Day

Europe:
J. Schmidt
R. Traquair (fossil fishes)

Africa:
G. A. Boulenger
J. Pellegrin

South America:
*C. H. Eigenmann

Australia:
E. R. Waite
W. MacLeay
D. G. Stead
A. R. McCullough

Indo-Australian Archipelago:
P. Bleeker
Max Weber

World at large:
D. S. Jordan
A. C. L. Gunther
C. Tate Regan
F. Steindachner
A. Smith Woodward (fossils)

In marine fishes geographic isolation exhibits largely different phases from the isolation of mammals and birds on the continents. The complete isolation in streams and rivers of fresh-water fishes corresponds with island isolation or insulation among birds and mammals. The most recent treatment of this great subject is that of C. Tate Regan in his notable address, "Organic Evolution," as president of Section D, Zoology, before the British Association at Southampton last year. He treats the very phenomena we are considering in their bearing on the older and more recent theories of the causes of evolution, which are not under consideration in this paper. G. K. Noble (1926) remarks that, from the genetic standpoint, isolation brings about inbreeding and would tend to change a heterozygous community into a homozygous one; he believes that there is no experimental proof for the action of isolation in the manner Regan assumes, but that, on the other hand, there is good proof that *isolation produces a change in fixing incipient races which have arisen genetically and which would otherwise be swamped.*

Amplifying Regan's summary of the *effects of physical environment* on the origin of species in fishes is the record of observations especially prepared for this paper

by Dr. E. W. Gudger, bibliographer and associate in the department of fishes of the American Museum, as follows:

From an early period the number of vertebrae in fishes has been used in the description and classification of fishes and in more recent time an increasing number of observations on temperature, salinity and skeletal speciation has been made:

(1) Günther in 1862 showed that the *Labridae* of temperate regions had more vertebrae than those living in warm water.

(2) In the following year Gill reviewed Günther and confirmed this observation for *Acanthopterygii* and *Malacopterygii*, and in 1864 he illustrated the doctrine by citations of species of the genus *Sebastes*.

(3) The field was widened by Jordan in 1885, by Jordan and Goss in 1889 in classifying the flounders and soles (*Pleuronectidae*), and by Jordan and Evermann in 1891 in classifying the *Serranidae*.

(4) In 1891, 1893 and 1894 Jordan made the following generalizations of forms with the most vertebrae:

Primitive forms:

Amphioxus	50–80 segments
Lampreys	100–150
Sharks	120–150
Ganoids	60–110

Cold water and tropical Teleosts:

Herring	56–41 vertebrae
Blennies	38–40 to 23–25, etc.
Flounders	60–30

Shallow water and deep sea Teleosts:

Gadidae	*ca* 50
Grenadiers	65–80

Pelagic forms more than shallow water:

Mackerels	31–50
Littoral forms	24–26

Freshwater more than salt:

Centrarchidae	30
Serranidae	24

To sum up: Northern, cold, deep waters (1, low temperature, 2, darkness, 3, monotonous life)—many small primitive vertebrae; southern, warm, shore waters—few, large, specialized vertebrae.

(5) In 1905 Jordan published an article, "The Origin of Species through Isolation," in which he vigorously argued for this principle, backing up his contention with a wealth of illustrations not merely from fishes but from other animal forms as well.

(6) Among the data supporting Jordan's contentions are:

(a) The Pacific coast *Leptocottus* shows constant increase in vertebrae from California to Alaska.

(b) Atlantic salmons and trouts form a marked group with few species, due to few barriers in a country geologically old. We note that of the Char (salmonoid fishes of the genus *Salvelinus*) and of *Coregonus*, different species occur in each isolated lake in Scotland, Germany and Scandinavia. But there are exceptions [Regan, 1923].

(c) Landlocked salmon is a new species due to isolation in the eastern United States.

(d) Among Pacific *Salmonidae* a new species arises in each creek and lake, especially in a geologically new country with many new barriers.

(e) The supposed more numerous American species are due to the energy of American ichthyologists in giving names [Regan, 1926].

(7) Hubbs experimentally found seasonal variations in large broods of minnows, with more caudal vertebrae and more fin rays in the cold season.

(8) Regan finds evidence that slight differences in average number of vertebrae in closely related species may be in part directly due to environmental influences.

(9) A definite illustration of the selection principle is that adduced by Thienemann in 1911 and 1912 of *Coregonus fera*[4] from Bodensee in Laacher See, Germany, which after forty years disappeared, leaving a new species, *C. sancti-benedecti*, with gill rakers twice as long and thickset. In the Bodensee this species feeds on crustacea and mollusca living on the shallow lake floor; Laacher See is in the crater of an extinct volcano, with steeply falling-away shores and no shore-dwelling fauna to serve as food, so that *Coregonus* had to feed on plankton; the modified gill rakers which developed to catch this food are sufficient, with certain outward bodily modifications, to constitute a new species.

Supplementing the above notes by Dr. Gudger is a summary by John T. Nichols, associate curator of the American Museum of Natural History:

(1) *Marine.* As a rule, isolation pertains among fishes to a less extent than among other groups, hence we have very wide ranges for faunal groups and, in many cases, for individual species. Taking the world as a whole, tropical marine fishes are less isolated than are those of the northern oceans. Essentially the same tropical fauna extends from the east coast of Africa across the Indian Ocean and into the Pacific. A warm current which passes the Cape of Good Hope against the wind has also given it access to the warmer parts of the north and south Atlantic, so that very similar fishes occur in the tropics around the world. The wide expanse of landless ocean between the most easterly islands of Polynesia and the American coast has been comparable as a barrier with the more or less temporary isthmus between North and South America, so that certain Atlantic species are found either identical or little changed on the Pacific side of the American continent which are not found further westward in the Pacific. In most cases isolation has developed in such species slight or average differences which may perhaps best be looked upon as racial.

(2) *Colder Marine.* In contrast, the faunae of colder north Atlantic and north Pacific are quite unlike. Several families are abundant in the Pacific which are not represented in the Atlantic (such as Greenlings) and the numerous genera of Pacific Sculpins and Flounders are for the most part peculiar to that ocean. That this is the result of isolation is emphasized by the fact that as one goes northward in the Pacific to sub-Arctic and Arctic waters, far northern forms are again identical with, or very close to, those of the Atlantic, by reason of free water connection around the Pole.

(3) *Deep Sea.* Though highly specialized for their peculiar environment, fishes of the depths show great similarity the world over, due to a lack of barriers between the ocean depths of one part of the world and of another. As we approach high latitudes in the southern hemisphere, marine shore fishes are peculiar—entirely different from those found anywhere else. There are many species which show a certain similarity to the northern Sculpins, but this is now understood to be parallelism due to parallel environment. They belong to the entirely unrelated family Nototheniidae.

[4] The LaacherSee *Coregonus.* In Regan's lecture, "Museums and Research," published in "Animal Life and Human Progress," 1917, he gave this as an example of the need for correct determination, the supposed evolution being due to the selection of the wrong species as ancestor.

(4) *General.* Specialized fishes of peculiar specialized environments, such as the deep-sea or the torrents or mountain regions, show two things: First, a high degree of specialization correlated with the environment; second, clear relationship to less specialized forms in less specialized environments. The deduction is obvious: They are descended from these less specialized forms; their migration to these environments has been the cause of evolutionary change.

(5) *New Environment.* We have not far to seek for cases where fishes have invaded a new environment, and, where they have become thoroughly established, there they are different. Marine Gobies and marine Herrings have invaded fresh-water, the Gobies notably in the West Indies, the Herrings in Africa (genus *Pelonula*, etc.), and we have fresh-water genera of these groups. In such cases, however, it is often not possible to say whether the new environment has brought about the change or has preserved the fresh-water forms from a certain amount of change which is doubtless continually in progress, due to competition in the old salt-water environment. All we see is that the fresh-water forms which have unquestionably come from the salt water are now different from the salt-water forms.

(6) *Salmonidae.* Of fresh-water fishes the Trout are peculiarly plastic, so that those in any one river are recognizably different from those in an adjoining piece of water. Isolation probably plays a part, but the slightly different environment does also, and how firmly their characters are implanted on the germ-plasm it would be difficult to say.[5] The retreat of the ice left descendants of the Arctic Char (such as the Golden Trout) insulated here and there in New England lakes; this insulation enables us to recognize them as distinct species or at least sharply marked races which, however, for all we know, may be duplicated somewhere in the wide northern range of the parent fish if the environment is exactly duplicated. As trout run into the swift cold water of high altitudes, their scales decrease in size and they become more highly colored, a condition which is found in its extreme in the one or more species of Golden Trout of the California Sierras. The condition has doubtless been emphasized by the fact that these upper waters are here isolated by falls. What we do not know is how much, if any, tendency these fish would show to revert to the parent form were they removed for any considerable period of time from their specialized environment.

Discoveries relating to the Origin of Species in Amphibia and Reptilia

Owing to restricted habitat and persistent intermediate function between aquatic water-breathing, and terrestrial air-breathing, life, *external specific* and *generic characters in amphibia are far more sensitive to local* or *geographic isolation than the higher vertebrates.*

[5] The transfer of eastern brook trout to western waters, as of Colorado, produces no immediate environmental change of color or form. (H. F. O.)

The following are the herpetologists who have made outstanding contributions on the continents in which they are interested:

North America :
E. D. Cope
John Van Denburgh

Africa:
G. A. Boulenger
F. Nieden

Asia:
L. Stejneger
O. Boettger

South America:
E. D. Cope
G. A. Ruthven

Indo-Australia:
P. N. Van Kampen

Europe:
G. A. Boulenger
E. G. Boulenger

Australia:
Dene B. Fry
F. Werner

As summarized by Noble in notes supplied for this paper, in Amphibia from the standpoint both of the field naturalist and the geneticist:

(1) Isolation produces species origin or speciation. This isolation is especially subtle under certain conditions. If species are found in the same locality they may differ (a) physiologically, as, for example, have different breeding habits: (b) in habit preference, one selecting drier ground, etc., than another; or (c) in size, as exemplified in *Plethodon.* (2) Whenever a species crosses a barrier it meets new conditions; *i.e.,* the sieve of natural selection changes. It is remarkable that in spite of the different selection sieves on the various East Indian and West Indian Islands the same species ranges through many of them. In the West Indies the same species of lizards and snakes (*e.g., Typhlops, Mabuya,* etc.) range through many islands without subspecific change, whereas other groups (especially terrestrial and arboreal ones) such as the frogs (*Hylodes*) tend to split up on each island; thus some insular species are stable and others plastic. (3) Species may arise within the range of an ancestral stock by physiological isolation. For example, female toads are attracted towards the male by his voice; if a change in the voice of the male should occur (as a mutational, a genetic difference) he probably would not attract a female, but if he should happen to seize a female, their offspring could only interbreed, for the voice of the offspring of the mutant would not be attractive to females of the original stock. (4) Most species are genetically complex and comprise hundreds of small mutations.

Intergrades in Amphibia

Noble (September, 1926) adds the following observations on intergradation and speciation in amphibians: Many wide-ranging species of Amphibia break up into different races or subspecies in different parts of the species range. In almost all cases the various subspecies intergrade with the other races of the species occupying contiguous ranges. A good example of this is to be seen

in the commonest salamander in eastern North America, *Desmognathus fuscus.* This species breaks up into the five well-recognized forms: *fuscus, auriculatus, brimleyorum, carolinensis* and *ochrophaeus.* In parts of the Adirondacks exact *intermediates* [intergrades] between *fuscus* and *ochrophaeus* occur. At Flatrock, N. C., perfect intermediates between *fuscus* and *carolinensis* are found, as shown by the collections in the American Museum. Similarly, the intergrades between the other subspecies occur in regions where the ranges of two forms meet.

Intergrades between the races of other species of urodeles have often been described. This is especially true of the subspecies of the Red Salamander, *Pseudotriton ruber,* of the Worm Salamander, *Batrachoseps attennatus,* and of the races of both the European and American newts. In fact many systematists distinguish a subspecies from a species solely on the basis that it intergrades with its closest relatives.

In the Salientia subspecies, or as we may now define them, *intergrading races,* are numerous but not always distinguished by a name. One of the most careful studies on the subspecies of a frog is that made by Boulenger[6] on the edible frog, *Rana esculenta.* Boulenger recognizes five intergrading races extending across Europe, Asia and North Africa. All the races except *R. lessonae* have a more or less definite range, but intergrading and apparently interbreeding occur between the different subspecies where their ranges meet or overlap. This is true even of the most clearly defined races. Boulenger[7] states: "The typical form is completely connected with the *var. ridibunda,* and where the two coexist in a locality, annectant individuals may be regarded as the result of crossing, such as undoubtedly must take place."

Mutations in *Amphibia*

Not all the species of Amphibia have arisen by a gradual evolution from subspecies occupying different ranges.

[6] 1918, *Ann. Mag. Nat. Hist.* (9) II: 241–257.

[7] *Loc. cit.* p. 254.

Very often two species differing only in a few pronounced structural differences will be found to occupy the same range. In these cases an examination of the group as a whole reveals that the derived form has arisen *in situ* by one or more sudden changes (*i.e.*, mutations). Thus the species of *Dendrobates* differ from those of *Phyllobates* merely by lacking the maxillary teeth. The species of *Nyctimantis* are merely hylas with a vertical instead of horizontal pupil. The salamander *Leurognathus marmoratum* agrees closely in external form and color with its immediate ancestor *Desmognathus quadramaculatus,* but it has suffered a great flattening of the skull, a loss of the vomerine teeth and the reduction of various skull foramina. *Manculus* is merely a dwarf form of *Eurycea bislineata cirrigera* which has lost the fifth or outer toe. There is abundant evidence in both the Plethodontidae and the Hynobiidae that the outer toe is usually lost at a single step (*i.e.*, mutation) and not by a gradual dwindling away. There are also many cases where maxillary or vomerine teeth may be lost at one step, for both ancestral and derived forms may live side by side and agree otherwise in almost the minutest detail (as, for example, in the species of Cacosternum).

Conclusion, Noble. Evolution in the Amphibia has not always been gradual and progressive in time and space. Pronounced and sudden changes, whatever be their origin, have also occurred. This is in full agreement with the geneticists' data. Large mutations of the magnitude of generic differences occur in the laboratory but are far less numerous than the small mutations—the material out of which subspecies are made.

Intergrades in Reptilia

Among the outstanding cases of intergradation in reptilia is that among the lizards of the genus *Chalcides,* as reviewed by E. G. Boulenger. Referring to Major Stevenson-Hamilton's paper on the geographic distribution of African mammals, it is pointed out that *one would be justified in treating some of the varieties as distinct spe-*

cies were it not for the existence of intermediate forms. Boulenger continues with notes on the classification and distribution of the Skink *Chalcides ocellatus,* "a species inhabiting southern Europe, northern and northeastern Africa and southwestern Asia, which present an extraordinary amount of variation: in fact, the structural difference between the two extreme forms is so great, that, *were it not for the wonderfully complete manner in which they are connected, they could not possibly be denied specific rank*" (italics my own). In other words, because of the existence of intergrades, specific rank is denied.

Continuing, Boulenger writes:

> In papers written nearly 30 years ago my father, dealing with the matter, came to the conclusion that this species could be divided into five distinct varieties or subspecies, characterized mainly by the coloration and by the number of scales round the body, which was found to vary between 24 and 40—a range of variation far greater than is to be found in any other lizard. The five forms then described were the *forma typica,* and the varieties *ragazzii, tiligugu, vittatus,* and *polylepis.* To these must be added the var. *occidentalis* (*Ch. simonyi* Stdr.).

The intergradations are observed in the following specific characters: (1) position of nostril, (2) slenderness of the body, (3) breadth of the scales, (4) proportions of limbs and body. *Isolation* is observed in the insular form on the island of Linosa distinguished from those of Tunisia and Malta by the following characters: (1) spotting, (2) paler or more intense colors, (3) number of scales; and Boulenger concludes that "these lizards are undoubtedly distinct from all the other forms of the species *C. ocellatus*" and proposes for them the varietal name of *C. o. linosae.* As to the effect of isolation and insulation in *Chalcides* he observes:

> In all, therefore, we have, apart from the typical form, seven varieties of the lizard *C. ocellatus,* and it is interesting from the evolutionary point of view that they are geographically connected, it being possible to trace every link in the chain from the short and stout variety with as many as 40 scales from Morocco, which must be regarded as the most generalized form, to the long and slender type with only 22 scales round the body from Abyssinia and Somaliland.

He proceeds to define the eight varieties or subspecies into which *C. ocellatus* may be divided, *e.g., C. o. poly-*

lepis, C. o. occidentalis, C. o. vittatus, C. o. tiligugu, C. o. typica, C. o. linosae, C. o. ragazzii and *C. o. bottegi,* and concludes with a map showing isolation and insulation distribution and with comparative figures of the two extreme forms and supposed relationship and distribution.

1859–1926. Discoveries Relating to the Origin of Species, Subspecies and Mutations in Birds

Due to the early interest of naturalists, we note that birds were comparatively well known in Darwin's time. A brief estimate of the increase in our knowledge of birds of the world since Darwin's time is as follows:

1871—Gray's list:	1,500 genera,	11,162 species
1909—Sharpe's list:	2,810 genera,	18,939 species and subspecies
1926—Chapman's list:		24,000 " " "

Ornithologists who have contributed data on the problem of speciation as affected by isolation and insulation are the following:

North America:
J. A. Allen
R. Ridgway
C. H. Merriam
J. Grinnell

West Indies:
C. B. Cory

Central America:
Salvin and Godman
R. Ridgway
Bangs
Griscom

South America:
P. L. Sclater
O. Salvin
von Berlepsch
Chapman
C. E. Hellmayr
Todd

Africa:
R. B. Sharpe
G. E. Shelley
A. Reichenow
W. L. Sclater
Chapin

Madagascar:
E. Oustalet

Indo-Malaysia:
W. T. Blanford
E. W. Oates
Rothschild and Hartert
Stuart Baker
T. H. D. La Touche
Oberholser
Bangs
McGregor
Stresemann
Robinson and Kloss
Delacour

Australia:
J. Gould
G. M. Mathews

New Zealand:
W. L. Buller
Rothschild and Hartert

Melanesia:
Rothschild and Hartert

Polynesia:
Rothschild and Hartert
Murphy

Palaearctic Region:
H. E. Dresser
E. Hartert
E. Stresemann
Witherby
Kleinschmidt
P. P. Sushkin
Kuroda

World at large:
J. Gould
R. B. Sharpe
A. R. Wallace

Species-Origin Environmental and Mutational in Birds

Chapman and Stresemann have recently discussed independently the subject of the factors of environment and mutation in relation to the origin of species in birds. Referring to the principle of direct environmental action Chapman, 1923[8] (pp. 243–4, 272–3), observes in a passage freely quoted, italicized and emended by the present author:

With enormous series of wide-ranging species at his command, the ornithologist is in possession of material to determine the character and extent of the variations in color and in size exhibited by what is obviously the same species. When to this intensive laboratory investigation he adds a knowledge of the environmental conditions under which the species exists, he can often definitely correlate effect and cause.

Thus, the ornithologist finds large forms occupying colder areas, dark ones humid areas, and pale ones arid areas; and *as the [environmental] conditions which obviously produce these variations in size and color merge one with the other, so do the [subspecific] forms themselves intergrade.* That these variations are inherent [*i.e.*, germinal, constitutional, hereditary] and not merely the temporary impress of [physical] environment on the individual is apparently shown by the fact that they are often as well marked in the nestling as in the adult.

While my experience as a collector and "museum man" has convinced me of the profound influence exerted by observable environmental factors (chiefly climatic) on the species, it has also brought to my attention certain instances in which I believe species have arisen by what is termed "mutation," that is, the appearance of characters, great or small, which apparently are the expression of an inherent tendency to vary rather than of environment. Such characters are commonly termed "individual variations." They may be manifested by a greater or lesser number of individuals in widely separated parts of the range of the species, and their perpetuation evidently depends upon their frequency and, especially, on an environment which affords sufficient isolation to ensure their preservation. . . .

Briefly, we have two groups of birds in the genus *Buarremon*, the members of which are distinguished from one another, primarily, by having a chestnut or a black and gray or black crown and, secondarily, by the presence or absence of a black pectoral band. It is this black collar which is the principal mutant character and which . . . appears or disappears purely as an individual variation and without relation to external influences. Its perpetuation or establishment as a specific mark does, however, depend upon environment expressed in what is doubtless the *most important external agent in promoting evolution—that is, isolation.* . . .

[8] Frank M. Chapman: "Mutation Among Birds in the Genus *Buarremon*." *Bull. Amer. Mus. Nat. Hist.*, Vol. XLVIII, Art. IX, pp. 243–278, October 15, 1923.

Summary. 1. The range of species of the genus *Buarremon* having a black and gray head and a breast-band are, with one possible exception discontinuous. Between the ranges of the northern and southern species, forms without a breast-band occur. 2. Although representative and closely related, none of the forms of this section is known to intergrade and, taxonomically, they therefore may rank as species. . . .

Conclusions. 1. That, although differing from the members of Section A of Group II in possessing a black breast-band, the members of this section are nevertheless representatives of the members of that section. 2. That the differences between the members of Section A and Section B are due to mutation. 3. That the differences between the members of Section B are in part due to the direct action of environment, in part to mutation, both being made effective by isolation.

Summary. With the extensive collections of South American birds at his command, carefully recorded as to exact locality and life-zone, Chapman observes a distinct case of mutation within the genus *Buarremon* in the presence of a black pectoral feather-band, which is established as a specific character by isolation or geographic discontinuity. Like the single case of black dorsal barring observed within the genus *Troglodytes,* the mutation does not intergrade and is thus recognized as of discontinuous or mutational origin.

Stresemann on Mutations

Stresemann, in his "Mutationsstudien I–XXV," also finds partial melanism as well as albinism arising as not infrequent mutational characters in *Anser, Accipiter, Egretta, Chlorophoneus* (*e.g., C. multicolor,* mut.= *C. nigrithorax* of Togo), *Lanius* of south China, *Sylvia* of Madeira, *Rhipidura* of New Zealand and Australia, *Accipiter* of New Guinea, an albinistic mutant. Stresemann concludes:

Die nunmehr erfolgende Zusammenfassung der wichtigsten Ergebnisse meiner vor drei Jahren begonnenen Mutationsstudien soll keineswegs ankündigen, dass der Stoff erschöpft ist und die Untersuchungen des Gegenstandes eingestellt werden müssen. . . .

Je länger wir uns mit diesem Gegenstande beschäftigten, desto mehr hat sich in uns die Ueberzeugung befestigt, dass den grossen Mutationen für die Veränderung des Artbildes eine hohe Bedeutung zukommt. Von Rotbraun zu Schwarz (= Grau = Blau), von Schwarz (Grau, Blau) zu Weifs kann nur ein Sprung führen; viele auffälige Zeichnungen sind höchstwahrscheinlich ebenfalls plötzlich in aller Vollkommenheit (und nicht allmählich durch gehäufte Wirkung vieler kleiner Schrittchen) aufgetreten. . . .

Eines lehren den Systematiker und den Zoogeographen die gegenwärtig dichromatischen Vogelarten mit aller Eindringlichkeit: dass die Grösse des Färbungsabstandes geographischer Rassen durchaus keinen Massstab für den Grad der Verwandtschaft und die Dauer der räumlichen Trennung bildet; und diese Erkenntnis muss dazu führen, den Artbegriff weiter zu fassen, als dies in der Regel bisher geschehen ist.

Chapman on Zonal Speciation

While still a firm believer in the importance of isolation as a factor in the development of new forms (*i.e.*, subspecies), Chapman has now come to feel that isolation as a rule also implies change of environment and that the two combined are the most potent factors in speciation. His most recent views are presented in his "Distribution of Bird-Life in Ecuador," and may be summed up as follows:

(1) Where the environment remains the same, the fauna shows comparatively little change; where the environment is altered or a new environment is offered, evolution proceeds at a correspondingly rapid pace.

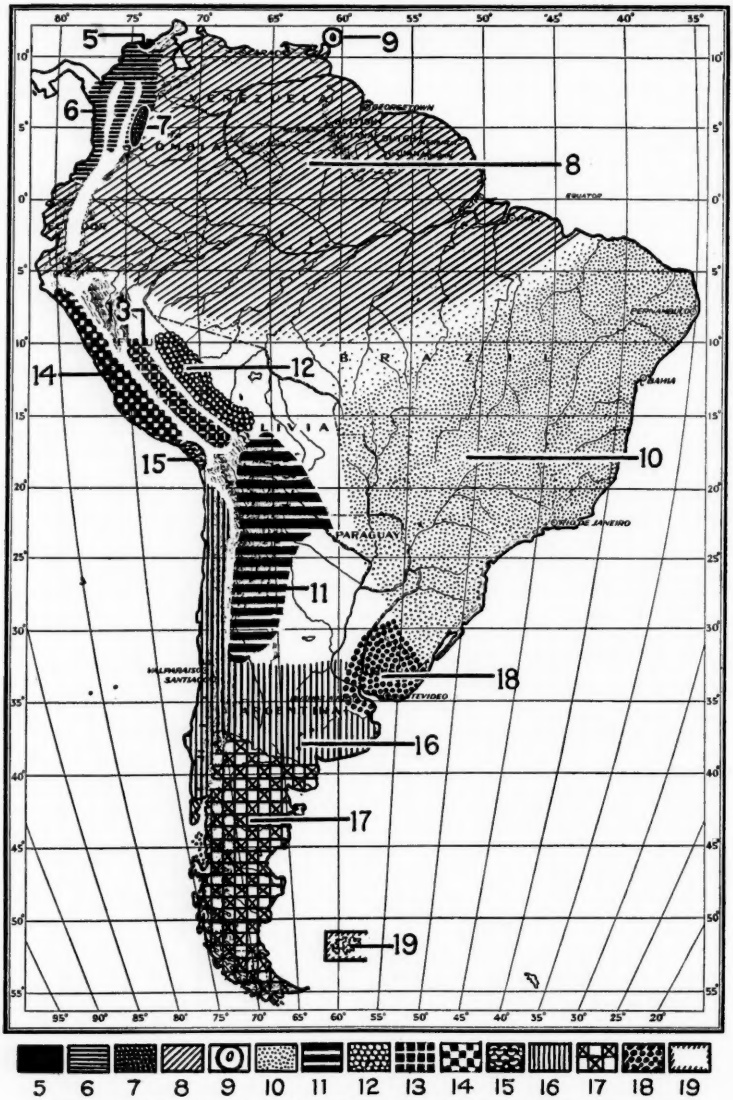
(2) Even when the life of one zone has been derived from that of an adjoining zone their faunas differ more widely than that of separated areas belonging in the same zone. . . . Change of environmental conditions without isolation is more productive of evolution than isolation without change of conditions.

(3) What more adequate tribute to the power of environment can one ask than to discover within this comparatively small but marvelously diversified country [Ecuador] one-fourth the birds of all South America and one-twelfth those of the entire world!

(4) Whether environment originates or whether, in the language of the day, it merely "starts something" by arousing latent potencies within the germ, the fact remains that organisms do respond to change and furthermore, that certain conditions, for example, humidity and aridity, almost invariably provoke the same type of response.

Speciation and Mutation of the South American House Wren (Troglodytes)

Corresponding with the field work of Osgood in North America on subspecies of the mammal *Peromyscus* is the field work of Chapman and Griscom on the House Wren (*Troglodytes musculus*) of Central and South America. The chief centers of speciation and subspeciation of this ubiquitous little bird are indicated in a zoogeographic map of South America (Fig. 3) which represents years



5 6 7 8 9 10 11 12 13 14 15 16 17 18 19

FIG. 3. Distribution of South American House Wrens. After Chapman and Griscom. 5, *Troglodytes m. atopus;* 6, *T. m. striatulus;* 7, *T. m. columbæ;* 8, *T. m. albicans;* 9, *T. m. tobagensis;* 10, *T. m. musculus;* 11, *T. m. rex;* 12, *T. m. carabayæ;* 13, *T. m. puna;* 14, *T. m. audax;* 15, *T. tecellatus;* 16, *T. m. chilensis* and, from the valley of Copiapo northward, *T. m. atacamensis;* 17, *T. m. magellanicus;* 18, *T. m. bonariæ;* 19, *T. cobbi.*

of close analysis (Chapman-Griscom, 1924) of very extensive collections. The total number of *Troglodytes* specimens collected and examined is 1,500, as compared with 30,000 of *Peromyscus*. Altogether, nineteen subspecies have thus far been recognized.

Those familiar with the marked physiography of South America, with (a) its cold and arid Pacific coastal belt, (b) its Andean Mountain chain subdivided by Chapman into four horizontal life-zones each clearly demarcated, (c) its vast Amazonian forest plain, (d) its pampas and plains of the Southeast and (e) its humid forests bordering the Straits, may anticipate wide speciation in this continent.

It is noteworthy that observers have discovered in *Troglodytes* only one instance of mutation in the sense of DeVries, which I shall speak of as D. Mutations, because there are no intergrades leading to it; this case is No. 15 on the South American chart and the supposed mutation consists of *broad bars crossing the dorsal feathers*. In other subspecies this character is only faintly indicated, absent entirely or a matter of individual variation.

At the writer's request in the month of May, 1926, Ludlow Griscom, assistant curator of birds, American Museum of Natural History, summed up his own opinions and theories as to isolation and speciation as follows:

(1) Granting the mutational possibilities existing in the germ-plasm, it can not be questioned that *isolation* is a most important factor in the speciation of birds, especially in its extreme form of *insulation* or island life. Isolation in birds brings about some degree of variation, even if not sufficient to give taxonomic or descriptive value.

(2) Insulation almost invariably produces speciation in direct proportion to the distance of an island from the mainland.

(3) Climatic isolation is a very important factor, but does not cause such extreme speciation as the insulation factor.

(4) In both factors of isolation and insulation, the time element from the geological point of view is of controlling importance.

(5) A second factor of similar importance is what might be called the relative plasticity of the particular bird. As a general principle, the more recent orders and families exhibit far more relative plasticity than older and more widely distributed groups.

(6) Isolation factors are more pronounced in the tropics than in temperate regions, due to the sedentary habits of tropical birds.

(7) Care must be taken to distinguish speciation within a faunal area due to isolation factors, from the speciation observed by passing from one faunal area to another.

(8) The evidence as far as birds are concerned is to the effect that a change of habits is a secondary and never a primary cause in speciation.

Griscom illustrates the above principles as follows:

(1) (a) In the classic Darwinian case of the finches (*Geospiza*) of the Galapagos Islands, the degree of speciation probably depends on the geologic time that has elapsed since the islands were separated from each other as well as from the mainland. (b) The very slight differences recorded in some of the smaller land-birds of Newfoundland indicate a relatively brief period of geologic isolation, combined with the migratory habits of the birds themselves, which further reduces the possible influence of their insular breeding-grounds. (c) In the case of Cozumel Island off the coast of Yucatan, we are certain that the insulation and isolation began in Pliocene time at the latest; the consequent speciation is very pronounced, and we are here dealing with birds of absolutely sedentary habits.

(2) Geographic isolation is the main element even where climatic conditions remain similar; *e.g.*, the climate of the recently studied Island of Cozumel is exactly similar to that of the adjoining mainland of Yucatan, yet insular speciation has advanced to a remarkable degree. Similar observation is that of Miller on the *Traguline* deer of the East Indies.

(3) The factor of plasticity is well illustrated in the House Wrens of South America, already cited, and in the Song Sparrow (*Melospiza melodia*), which in North America divides into over twenty subspecies. This may be contrasted with the more stable Killdeer (*Oxyechus*), which in the same region presents no subspecific variation. Plasticity, however, would seem to be of less importance in the Tropics than in temperate regions.

In conversation with Griscom and with the eminent French ornithologist, Jean Delacour, some of the exceptions were noted where geographic isolation is not attended by geographic variation or speciation:

(1) Land birds and perching birds of widely migrating habits do not tend to speciation; *e.g.*, the bank swallow or sand martin, the only small Passerine bird common to both the New and the Old Worlds which exhibits no appreciable variation.

(2) Certain species of ducks of world-wide and discontinuous distribution are excellent examples of birds which do not show any specific variation. In general, older and more primitive birds do not tend to speciation; *e.g.*, tree ducks (*Dendrocygna*), a subfamily now dying out.

1859–1926. DISCOVERIES RELATING TO THE ORIGIN OF SPECIES IN MAMMALS

Before and after Darwin there is an honor roll of mammalogists, who have been observing and collecting mam-

mals all over the world and whose publications have furnished and will furnish data for purely biological treatment, although perhaps they themselves have not made biological use of their material. For convenience of reference they may be listed by countries in alphabetical order, without any question of seniority or importance:

	J. A. Allen	J. Grinnell	E. W. Nelson
	G. M. Allen	E. Heller	W. H. Osgood
	H. E. Anthony	N. Hollister	T. S. Palmer
	J. J. Audubon	A. H. Howell	E. A. Preble
NORTH AMERICA	J. Bachman	H. H. T. Jackson	S. N. Rhoads
	V. Bailey	M. W. Lyon, Jr.	F. B. Sumner
	E. Coues	E. A. Mearns	W. P. Taylor
	D. G. Elliot	C. H. Merriam	F. W. True
	E. A. Goldman	G. S. Miller, Jr.	

Of these, the most important philosophical contributions have been made by Joel A. Allen on geographic distribution, isolation, climatic evolution; by C. Hart Merriam on principles of humidity and temperature control and subspecific variation; by Gerrit S. Miller on geographic isolation, insulation, variation, speciation; by Wilfred H. Osgood on subspeciation, especially in *Peromyscus;* by Francis B. Sumner on biological analysis of subspeciation.

South America. Following the work in South America of such pioneers as Azara and Humboldt are the important observations on geographic isolation, variation, and speciation, of the following authorities, supplemented by the field work of Edmund Heller and others:

	Einar Lönnberg
J. A. Allen	W. H. Osgood
H. E. Anthony	R. A. Phillippi
Outram Bangs	O. Thomas

Europe. All the earlier contributors to European mammalogy are listed in Miller's "Mammals of Western Europe." The fullest analytical treatment of geographic isolation and variation among European mammals is found in the same work. Europe, with its relatively restricted area and fauna, devastated by civilization, does

not lend itself to biological discussion in the manner of Africa, Asia, North America or Australia, where the natural wild faunae may still be studied. Among leading contributors are the following mammalogists:

K. Andersen	R. Lydekker	R. I. Pocock
A. Cabrera	P. Matschie	O. Thomas
W. H. Flower	Gerrit S. Miller, Jr.	E. L. Trouessart
E. Lönnberg		H. Winge

Asia. The field naturalists and museum workers who have made and will make important contributions in the way of collections and of taxonomic analyses are chiefly the following:

W. L. Abbott	C. M. Hoy	N. Nassonov
G. M. Allen	C. B. Kloss	H. C. Raven
R. C. Andrews	G. S. Miller, Jr.	P. P. Sushkin
N. Hollister	A. Milne-Edward	O. Thomas
		R. C. Wroughton

Philosophic discussion of speciation among Asiatic mammals after the manner of P. P. Sushkin's work on the birds is still to come.

Africa. The earlier explorers, collectors and naturalists in Africa enumerated in the volumes of Sclater include many priceless observations of now extinct species like the Quagga, which must be considered in the marked *north to south* speciation characteristic of Africa, in contrast to the *east to west* speciation characteristic of Asia, North America and Australia. Among earlier and more recent contributors to mammals are the following:

J. A. Allen	E. Heller	A. Roberts
J. Anderson	N. Hollister	T. R. Roosevelt
J. V. B. du Bocage	H. Lang	K. H. Satunin
J. L. Bonhote	E. Lönnberg	P. L. Sclater
J. F. Brandt	R. Lydekker	Stephenson-Hamilton
A. Cabrera	P. Matschie	O. Thomas
W. E. De Winton	A. Milne-Edwards	E. L. Trouessart
G. Dollman	R. I. Pocock	R. C. Wroughton

Of these, Lydekker, Matschie, Pocock, Hamilton and Thomas have made some of the most notable contributions to geographic and climatic variation and speciation.

Speciation of the Deer Family around the World on the Northern Parallels

On a new equal-area map of the world arranged for zoogeographic and paleogeographic plotting, it may be shown as a first principle that *geographic separation, migration and isolation frequently but not invariably lead to subspeciation and thus finally to speciation.*

To Darwin in 1837–1859 were known only two species of stag (*Cervus elaphus* and *Cervus canadensis*), one species of moose (*Alces machlis*) and one species of reindeer (*Rangifer tarandus*). Then, as now, these species occupied three great transverse geographic belts, *Cervus* in the southern, *Alces* in the central, *Rangifer* in the northern parallels, extending from North Temperate to Arctic regions. As collected and observed from Scotland across Eurasia and North America to New Brunswick, *Cervus* yields twenty-three species and subspecies, *Alces* yields eight species and subspecies, *Rangifer* yields twenty-one species and subspecies. The more uniform forest and swamp environment of *Alces* yields fewer species than the highly varied circumpolar and boreal environment of *Rangifer* in its woodland and barren-ground groups, or than *Cervus* in its plains-bordering uplands, forests humid and arid, and high plateaus.

Zoologists disagree as to the taxonomic rank of these twenty-three subspecies of *Cervus,* but close museum comparison or field observation would prove that they are germinally separate, as in the case of *Peromyscus.* A notable subspecific case in *Alces* is *Alces americanus shirasi* Nelson, occupying the mountain sides bordering the western slopes of the Yellowstone Park in Idaho, Wyoming and Montana, and with conspicuous adaptations in hoof, horn, limb and pelt.

In discussing these not very obvious subspecific differences, Anthony observes that many of the alleged subspecific differences seem to be man-made, dependent on knowledge of actual geographic locality, not clearly separable, without geographic record even breaking down en-

tirely. He points also to instances of uniformity in very wide range of species like *Bison americanus,* which does not split up into many subspecies, or like *Felis concolor,* in which subspecific differences have been determined with great difficulty. Quite different is the case of the American *Ursus,* in which certain of Merriam's subspecies live side by side in the same region and may represent hybrids. We are, however, speaking only of subspecies which are widely separated geographically.

By contrast, the really germinal as well as somatic differences between the far-flung species of *Cervus, Alces* and *Rangifer* can not be challenged. As listed and plotted geographically by Anthony for the present paper, these three great antlered types of the North Temperate and Arctic plains, forests, mountains, barren lands and tundras, described as fifty-two species and subspecies in all, are distributed as to geography and as to climate as shown in the following table and map (Fig. 4).

CERVUS: STAG, DEER, WAPITI. EAST TO WEST RANGE

1. *Cervus barbarus*	Barbary deer	Morocco; Algiers; North Africa (Palearctica)		Chiefly arid
2. *Cervus corsicanus*	Corsican stag	Corsica and Sardinia		Semi-arid
3. *Cervus scoticus*[9]	Red deer	Great Britain and Ireland		Humid
4. *Cervus elaphus hispanicus*	Southern Spanish Red deer	Southern Spain		Humid and semi-arid
5. *Cervus elaphus bolivari*	Central Spanish Red deer	Central Spain		
6. *Cervus elaphus germanicus*	Red deer	Middle Europe		Humid
7. *Cervus elaphus atlanticus*	Norwegian Red deer	West coast Norway		Humid
8. *Cervus elaphus elaphus*	Red deer	Sweden		Humid
9. *Cervus maral*	Maral	Persia; Crimea; Caucasus	Chiefly forest	
10. *Cervus bactrianus*		Russian Turkestan		Chiefly arid
11. *Cervus cashmiriensis*	Kashmir deer; hangul	Vale of Kashmir and adjacent mountains	Chiefly forest, with open parks	Humid
12. *Cervus wardi*	Ward's stag	Tibet		
13. *Cervus wallichi*		Tibet		
14. *Cervus albirostris*		Tibet		
15. *Cervus macneilli*	Kansu stag	Kansu and Szechuan border		
16. *Cervus yarkandensis*	Yarkand stag	Eastern Turkestan		Mostly arid?
17. *Cervus songaricus*	Tian-shan stag	Tian-shan Mts.	Forest and alps	Mostly arid?
18. *Cervus sibiricus*	Altai maral	Baikal, Saiansk, and Altai Mts., Southern Siberia and northern Mongolia	Formerly forests and open timberless country—even in open alps on desert mts. Now restricted to forests and meadows	Extreme humid to extreme arid

[9] Scotch red deer taken to New Zealand has increased in size and in spread of antler—almost a subspecies in less than a century.—P. C. M.

19. *Cervus xanthopygus*	Bedford's deer; Manchurian stag	Manchuria, etc.—adjoining parts of Siberia	Forests	Humid
20. *Rangifer greenlandicus*	Olympic elk	Wash., Oreg., Calif., formerly s. to San Francisco Bay. Vancouver Is.?	Chiefly forested regions, with open meadows	Humid
21. *Cervus nannodes*	Dwarf elk	San Joaquin Valley, Calif., and adjoining foothills	Plains and tule swamps	Generally arid
22. *Cervus cervus merriami*	Merriam's elk	New Mexico and Arizona	Mts. and plateaus, forests and meadows	Generally arid, but wet forests
23. *Cervus canadensis*	American elk; wapiti	Southern Canada and U. S., including N. Y., N. J., Central States (Missouri, Nebraska, Dakotas, etc.), west beyond the Rockies, south to Virginia and Carolinas.	Open plains, badlands, sand hills; forests and meadows	Humid to extreme arid

ALCES: MOOSE. EAST TO WEST RANGE

1. *Alces alces germanica*	East Prussia and marshes of Pinsk, Poland.
2. *Alces alces niger*	European Russia and forest regions of the Yenesi.
3. *Alces alces alces*	Europe.
4. *Alces alces bedfordiae*	East Siberia.
5. *Alces gigas*	Alaska.
6. *Alces columbae*	British Columbia.
7. *Alces americana shirasi*	Wyoming.
8. *Alces americana americana*	Northeastern North America.

RANGIFER: REINDEER, CARIBOU. EAST TO WEST RANGE

1. *Rangifer tarandus tarandus*	Swedish Lapland.
2. *Rangifer platyrhynchus*	Spitzbergen.
3. *Rangifer fennicus*	Finnland.
4. *Rangifer tarandus pearsoni*	Novaya Zemlya.
5. *Rangifer tarandus sibiricus*	Siberia.
6. *Rangifer granti*	Alaskan Peninsula.
7. *Rangifer excelsifrons*	Northern Alaska.
8. *Rangifer arcticus ogilvyensis*	Ogilvie Mts., Yukon, Canada.
9. *Rangifer stonei*	Kenai Peninsula, Alaska.
10. *Rangifer arcticus arcticus*	Dist. of Mackenzie, Canada.
11. *Rangifer mcguirei*	Alaska—Yukon Boundary.
12. *Rangifer dawsoni*	Graham Island, Queen Charlotte Islands, Canada.
13. *Rangifer montanus*	Selkirk Range, British Columbia.
14. *Rangifer osborni*	Cassiar Mts., British Columbia.
15. *Rangifer fortidens*	Alberta, Canada.
16. *Rangifer pearyi*	Ellesmere Island.
17. *Rangifer caribou sylvestris*	Southwestern shores of Hudson Bay.
18. *Rangifer caribou caribou*	Eastern Canada.
19. *Rangifer arcticus caboti*	Greenland.
20. *Rangifer greenlandicus*	Newfoundland.
21. *Rangifer terranovae*	Labrador.

Probable Intergradation in Zebras and Foxes

R. I. Pocock writes, July 30, 1926:

I do not suppose that any one museum possesses a sufficient number of skins actually to prove ocularly the existence of intermediates [intergrades] between all the described forms of Burchell's Zebra. Personally I am, and have long been, of the opinion that such intermediates exist at the present time—the evidence is strongly in its favour. The intergradation between Grant's Zebra of British East Africa and Burchell's of the Orange Free State (I am here writing from memory, having no books to check

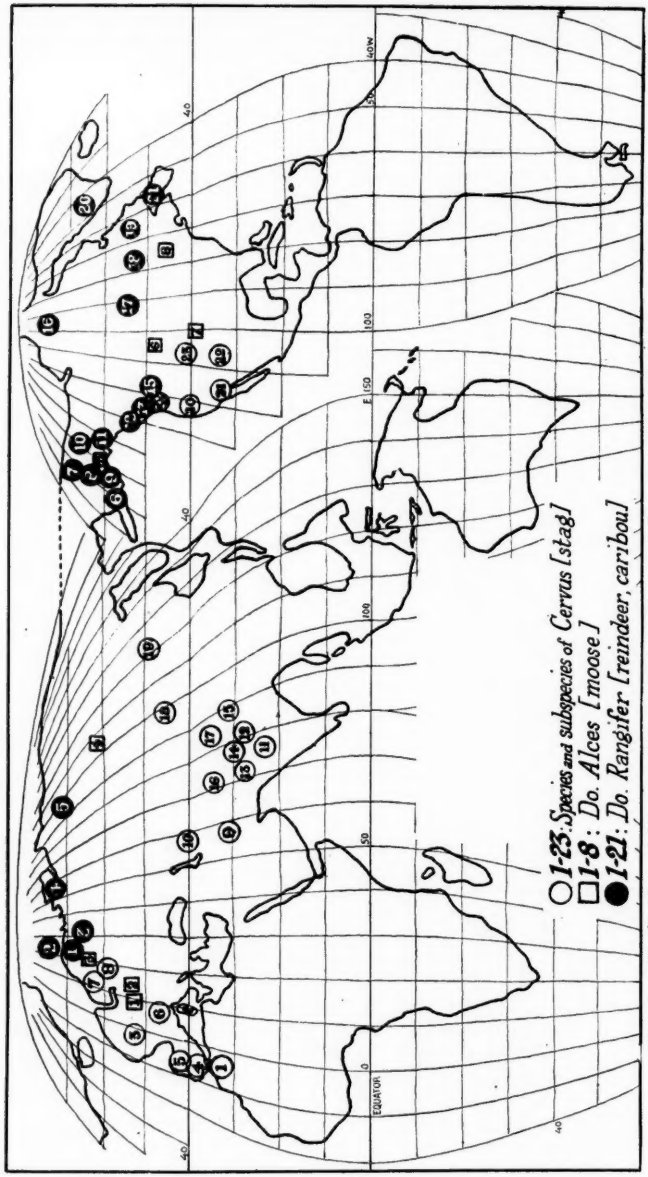


FIG. 4. Distribution of 52 subspecies of *Cervus*, *Alces* and *Rangifer*, on a homalosine world projection. ○=Cervus [stag]. □=Alces [moose]. ●=Rangifer [reindeer, caribou].

exact localities, and it is thirty years since I worked at the group) was almost complete, judging from the comparatively small amount of material I had then to judge from, and the gradation ran approximately as follows: Grant's, Selous's, Chapman's, Wahlberg's, Burchell's.

Since then one or two additional subspecies have been described, all serving to confirm the hypothesis. So far as living forms are concerned, we are here brought to a standstill. Nevertheless the differences between Grant's and Burchell's are very marked, more marked than the differences between Burchell's and the typical extinct Quaggas shown in Edward's coloured plate taken from life. From the evidence I was able to gather from photographs and other illustrations, I came to the conclusion that there were probably several subspecies of Quagga ranging in coloration from forms hardly differing from Burchell's to forms in which the obliteration of the stripes was almost completed by pigmentation of the intermediate areas and epigmentation, or depigmentation, of the stripes. So I did not hesitate to refer all these plateau zebras to *Equus quagga*—Grant's quagga, with its conspicuous banding of black and white, being the most primitive existing type.

If I had known you were after existing subspecific intergradations, I think I could have shown you some interesting cases. For instance, from skull measurements and skins I came to the conclusion a year or two ago that the small Punjab fox, *Vulpes leucopus*, is linked up through the Himalayan fox *V. montana* with typical *V. vulpes* of Europe.

Speciation of the Deer-Mice in Contiguous North American Areas

In contrast with the three far-flung genera of deer, the geographic and germinal separation of which is partly due to natural extinction or to elimination by man of intermediate forms, let us examine the Deer-mice or Prairie Mice of the genus *Peromyscus* of the central North Temperate region of North America, *in which certain of the intermediates or intergrades have not been eliminated.* This little animal is the best-known zoologically and biologically of any species of mammal in the world to-day, because of the monumental field work of Osgood, who has collected no fewer than 30,000 specimens in a decade, and the experimental biological work of Sumner, who approaches the problem of speciation and mutation from the highly trained genetic and experimental point of view of the school of Wilson and Morgan, with no preconceptions, with no affiliations, with no particular sympathy for American systematists.

Osgood's color map (*N. A. Fauna*, No. 28) exhibited the entire range of this polyform and polychrome rodent. The area which presents the best example of contiguous subspecies with intergrades is that of the central United States bordering on Canada and British Columbia, as

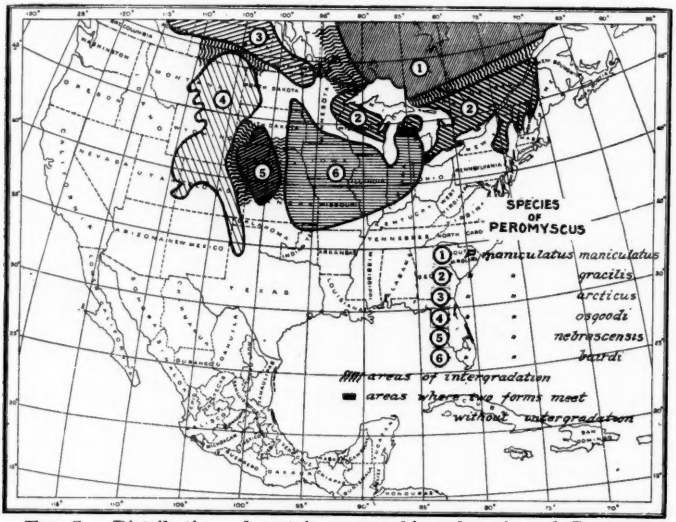


FIG. 5. Distribution of certain geographic subspecies of *Peromyscus maniculatus*. After Osgood, May 19, 1926. ∫ ∫ ∫ ∫ ∫ = areas of intergradation. ■ = areas where two subspecies meet without intergradation.

shown in Fig. 5, wherein the intergrades are explained by Osgood as follows:

"Typical *Peromyscus maniculatus* (No. 1) is of good size, stockily built and dark colored; in the east it intergrades only with *P. m. gracilis* (No. 2), which has a longer tail; in the west *P. m. m.* intergrades with *P. m. arcticus* (No. 3), which is about the same color but with slightly different proportions. *P. m. arcticus* then intergrades with *P. m. osgoodi* (No. 4), which is of paler color. *P. m. osgoodi* turns eastward and intergrades with *P. m. nebrascensis*, which is decidedly smaller, paler and shorter tailed. *P. m. nebrascensis* then grades into No. 6 (*P. m. bairdi*), which retains the characters of small size and short tail but takes on a decidedly darker color. Thus, by various stages *P. m. m.* (No. 1), a forest-dwelling form, evolves via Nos. 3, 4, and 5 into a prairie form (No. 6) with somewhat different habits.

"It is probable that under aboriginal conditions the Prairie Mouse was confined to the natural prairie and did not extend eastward beyond Illinois.

With the clearing and cultivation of the land, however, it has worked across Indiana and into Ohio, Michigan, and southern Ontario. Here it has met the natural range of *P. m. gracilis* (No. 2), and these two occur in different ecological niches throughout a considerable area. Within this area they appear as distinct species although, by different routes, they may be traced back to the same *P. m. maniculatus* form (No. 1)."

The area studied biologically by Sumner is that of the contiguous forests and arid regions of northern, southern and central California; recently he has also studied Florida and Alabama. He has also collected, but not reared, much material from Arizona. The numerous subspecies observed by Merriam and by Osgood have been accepted with great reluctance, especially by naturalists not familiar with the excessively sharp geographic and climatic barriers of the western United States. My own reluctance to accept these subspecies as of real germinal or genetic value has been entirely removed by the persistent, penetrating observations and experiments of Sumner, largely in the identical collecting grounds of Merriam and Osgood. We now welcome Osgood's observations as the most *convincing demonstration of the principle of continuity thus far afforded in zoological series, namely, continuity in subspeciation, which gives convincing proof of continuity in speciation.*

We may append the most recent expression of Osgood's views, June 8, 1926, taking the liberty of changing certain of his terms to conform with the language used in the rest of this paper:

(1) If there are any mammals which do not show differentiation [speciation] connected or coincident with geographic boundaries, they have not come to my notice. (2) With certain limitations on account of their constitution, I have little doubt that other vertebrates and at least the majority of plants show the same relation between differentiation and distribution as mammals. (3) I have tried to express this briefly by saying, "The existence of diverse inosculating units [intergrades] correlated with geography is characteristic of terrestrial vertebrates." This statement, of course, requires proof, but if made to the comparatively few zoologists who have wide acquaintance with animals in nature, does not encounter much opposition. (4) It is obvious, of course, that some animals are more wide-ranging without differentiation than others but most of those, like the puma (*Felis concolor*), which have been regarded as inflexible types, are now known to be subject to the same kind, if not the same number, of geographic variations [subspeciation] as the others, largely dependent upon the amount of

material available for study. Even the Polar Bear (*Ursus maritimus*) with its relatively uniform environment, is credited with four or five recognizable differentiations [subspeciations]. (5) The failure of some of the larger carnivores to develop numerous geographic races is perhaps not because they are less susceptible to change, but because their greater powers of locomotion offer greater opportunities for diverse matings and thus for the "swamping effect" of breeding. It is possible that Merriam's numerous subspecies of bears illustrate this point. Perhaps the large number of slightly characterized but still recognizable forms [subspecies] he is able to distinguish are only the result of an enforced isolation brought about by the extermination of the animals formerly inhabiting intervening areas and providing opportunity for cross-breeding [hybridizing] on a much larger scale than at present. It seems to me that the kinds of bears Merriam describes are different from the other species and subspecies we know, and if they require a special explanation, this may be offered as a possible one.

Isolation in the Origin of Localized Races of Peromyscus

Sumner's observations, beginning in 1915 and extending over eleven years, are of the utmost importance in adding the principles of genetics and experimentation to those of field zoology. While the so-called Merriam-Osgood subspecies are based on real and obvious differences, classification becomes like dividing the spectrum and depends upon the standard set (Sumner, 1917–Osgood). The Sumner-Osgood observations supplement each other. Sumner removes the suspicion which had prevailed as to the germinal reality of Osgood's subspecies and proves that we have real species-in-the-making, by continuous intergradations which link one climatic or environmental region with another, as follows:

(1) Both by repeated experiment and by the genetic analysis of hybridizing, the reality of subspecies is tested.

(2) Color mutations occur (Sumner, *Genetics*, Vol. 2, May, 1917; Sumner-Collins, *Journ. Exp. Zool.*, Vol. 36, Oct., 1922) but not in the main-line of evolution, which is continuous.

(3) Anatomical, proportional, and pigmental or color differences are found to be differences of degree (Sumner, 1918).

(4) Sumner, 1924.3. (1) The summary of eight years' experiment proves the comparative stability of subspecies of the Deer-mice (*Peromyscus*) under very marked new environmental physical conditions. (2) The Merriam-Osgood subspecies are proved to be stable under changed conditions of environment, by transplantation experiments, *i.e.*, a desert subspecies, *P. m. sonoriensis*, reared for eight years in the relatively humid environment of the southern California coast (La Jolla), is entirely unmodified in the direction of the local subspecies *P. m. gambeli*. This doubly proves that (a) characters of the desert *P. m. sonoriensis* are germinal, not

environmental, and (b) that humid environment makes no modification whatever toward increased depth of color, in eight years and in seven to twelve generations. (3) Similar results are obtained by the transplantation of *P. m. rubidus* from the highly humid northwestern coast of California to the relatively less humid coast of southern California. (4) These two introduced subspecies, therefore, fail to converge when reared alongside one another in the latter (intermediate) type of environment.

(5) Sumner, 1924.1. (1) Protective coloration is less urgent in nocturnal than in diurnal animals. (2) Protective coloration (*i.e.*, Selection) does not appear to explain color differences between nocturnal desert and humid subspecies. (3) Optical properties of background (*i.e.*, black lava rocks) are only doubtfully less responsible for color peculiarities which have been attributed to them by some naturalists (*e.g.*, Merriam, Osgood, Goldman). (4) Atmospheric humidity is prevailingly correlated with color depth in birds and mammals.

(6) Sumner, 1925.1, Huestis. Crossing of the desert *P. eremicus eremicus* and the humid *P. e. fraterculus* subspecies shows that all the subspecific characters follow the "blending" type of inheritance.

(7) Sumner, 1925.2. (1) Color differences used in defining subspecies are shown by experiment to be hereditary, consequently part of the speciation process. (2) There are strong reasons for doubting whether paleness of desert animals is chiefly due to Selection for concealment purposes. (3) There is some reason for attributing paleness or intensity of color to the direct or indirect effect of climatic environment on pigment formation acting through many generations.

(8) *Independent Characters.* Sumner in a recent paper (*Journ. Mam.*, 1926) and in a letter dated September 29, 1926, appears to have been forced to modify his early views regarding the inheritance of subspecific characters. He no longer takes the position "that the characters which distinguish subspecies from one another are fundamentally different from those which distinguish the various 'mutant' stocks which chiefly interest Mendelian workers. There is, to be sure, an obvious and striking *apparent* difference, which has been stressed by some taxonomists, and which greatly influenced me during the earlier stages of these studies. The characters of 'natural' races *seem* to be inherited in a strictly continuous fashion, while the characters of mutants are plainly inherited in discontinuous fashion. But I have been (I may say reluctantly) forced to the belief that there is probably no fundamental distinction here. It now seems to me likely that the 'multiple factor' theory satisfactorily accounts for the mode of inheritance of subspecific characters. Individuals indistinguishable in color characters from one or another of the parent races have already been recovered, even in a rather limited series of F_2 hybrids and backcrosses.

(9) "It is plain that these 'subspecies' have diverged from one another in respect to characters which have varied quite independently [of one another]. There is no single graded series for all the characters, which would lead us to suppose that they are in some way correlated or 'linked' together (AMER. NAT., April–May, 1918, pp. 205, 206). Certain differential characters of the component subspecies may, it is true, undergo simultaneous change throughout a part of the range of the species, but the asso-

ciation between these same characters is found to be entirely dissolved when we pass to other parts of its range (AMER. NAT., May–June, 1923, p. 239). Most of the elements comprised in the total subspecific complex have been found to be independent of one another in inheritance (*Journ. Exp. Zool.*, Oct., 1923, p. 272). As in my previous studies, I find no general tendency for the elements of the complex which distinguish one race from another to vary together within the single race. They may or may not do this. Thus, tail length and foot length, which have undergone parallel modifications in the evolution of some geographic races, are found to vary together in the same direction, even when the influence of body size has been eliminated from consideration. And certain of the pigmental characters, though not all, are likewise rather strongly correlated with one another. On the other hand, neither tail length nor foot length appears to be correlated with any pigmental character (*Journ. Mam.*, Aug., 1926). It seems to me obvious that these facts bear directly on the nature of the process by which one species is transformed into another."

Of our real ignorance of the causes of species formation Sumner[10] says: "We are not yet prepared to frame any adequate general hypothesis as to species formation. The Mendelian Mutation system of facts and theories appears to me to be no more successful in this respect than its predecessors."

Speciation in the Gopher, Thomomys

The most recent study of speciation under the influence of geographic distribution is that of Grinnell, who has made an intensive study of the pocket gophers of the genus *Thomomys* of California; he divides the state geographically into thirty-three specific and subspecific areas as shown in figure 6. He remarks:

The most universally distributed type of rodent in California is the pocket gopher. It is found thriving at and below sea level, around the southern end of Salton Sea in Imperial County, and above timber line, at 11,500 feet altitude in the vicinity of Mount Whitney; it is found from the arid desert mountain ranges of the Inyo region, such as the Panamint Mountains, to the rainy and foggy coast strip at Humboldt Bay and Crescent City; it is found in the yielding sands of the Colorado River delta at the Mexican line and on the Modoc lava beds at the Oregon line.

As to the seeming correlation of the distribution area of each race with a relative uniformity of environmental conditions, he concludes that (1) the inferior powers of locomotion of *Thomomys* has produced a condition of ex-

[10] "Discussion of the Origin and Inheritance of Specific Characters," 1923, p. 254.

FIG. 6. Distribution of species and subspecies of the Pocket Gopher, genus *Thomomys*, in California. After Joseph Grinnell, July, 1926.

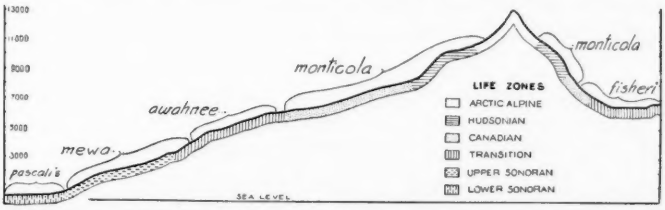


FIG. 6a. Sectional profile of the Sierra Nevada through the region of Yosemite, showing the location of the species and subspecies of the Pocket Gopher according to altitude and life zone.

treme provincialism, as it were; (2) influenced by the more or less impassable barriers here and there, each of

the many and diverse specific and subspecific areas has impressed its *stamp,* namely, a peculiar combination of adaptive characters best fitting that subspecies to its restricted area; (3) the evolution of the geographic habitats, or "differentiation areas," must have preceded the differentiation [speciation] of the *Thomomys* stocks which subsequently came under their impress.

Regarding the color gradations shown in the Plate used as the frontispiece to this article, Grinnell observes:

> The matter of coloration of gophers presents a rather baffling problem. Referring to the accompanying plate, which depicts eight of the thirty-three gophers of California, it becomes apparent that the paler colored forms are generally associated with arid habitats; the darker colored with humid habitats. *Bottae* of the coast belt as compared with the almost white *albatus* of the Colorado delta presents an extreme amount of difference. Is the factor which has to do with these diverse conditions of coloration, light, or temperature, or is it humidity of the air?

SUMMARY OF SPECIATION AND MUTATION AS OBSERVED IN LIVING VERTEBRATES

A summary of the conclusions drawn from the independent observations of many kinds of living vertebrates is practically contained in the writer's previous article, "The Problem of the Origin of Species as it appeared to Darwin in 1859 and as it appears to Us To-day." It appears that the problem of the age-long process of the origin of species can best be studied under the natural conditions of past and present time; it appears that all vertebrates which range into a new set of natural conditions, whether by geographic isolation or otherwise, in the course of time give rise to new specific forms; it appears that, where vertebrates can be traced from one geographic range as it merges into another, "transitional" or "intermediate" forms are observed, so that if placed side by side one subspecies passes gradually into another by *intergrades,* and thus the supposed barriers existing between species and subspecies disappear.

Speciation is a normal and continuous process; it governs the greater part of the origin of species; it is apparently always adaptive. Mutation is an abnormal and irregular mode of origin, which while not infrequently

occurring in nature is not essentially an adaptive process; it is, rather, a disturbance of the regular course of speciation.

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DO ALBINO RATS HAVING TEN GENERATIONS OF ALCOHOLIC ANCESTRY INHERIT RESISTANCE TO ALCOHOL FUMES?

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INTRODUCTION

THIS investigation deals with the effects of alcohol fumes upon the albino rat (Mus norvegicus albinus) with special reference to the inheritance of resistance to fumes in untreated descendants of ten generations of treated animals.

Administration of alcohol to animals in order to determine its effect upon germ cells and heredity has recently occupied the attention of a number of investigators *e.g.*, Stockard, Pearl, MacDowell and others.

During the past five years an experiment dealing with the effects of alcohol upon the albino rat has been carried on by Hanson and his students. For a detailed account of the general aspects of the experiment see the introductory paper by Hanson and Handy ('23).

This investigation included ten treated generations and corresponding controls. The individuals of each treated generation gradually acquired an increased resistance to alcohol during the period of treatment. Hanson and Handy have shown that rats sixteen days of age could be given only thirty minutes' treatment with 50 cc of alcohol evaporating in the tank, but as resistance developed, the time of treatment was extended and the amount of alcohol increased. At twelve months of age the rats could withstand four hours' treatment with 200 cc of alcohol in the tank. This increase in resistance was due in large measure, of course, not only to advance in age and corresponding increase in size, but also to some extent to a greater tolerance for alcohol, since adult rats, long past the growth period, still showed increases

in resistance under continued administration of alcohol.

The great-grandchildren of the tenth alcoholic generation afforded excellent material for testing experimentally whether the resistance acquired during the lifetime of individuals, generation after generation, was in any measure transmitted. The problem, then, was this: Do the descendants of treated rats, having ten generations of alcoholic ancestry, possess any greater power of resistance than the descendants of control rats of entirely non-alcoholic ancestry?

METHODS

For this experiment sixty rats of the thirteenth generation were available, thirty of which were descendants of control animals, thirty of treated. Each group of thirty included fifteen males and fifteen females. Five control males and five males of alcoholic ancestry were treated together in the same fume tank. There were, therefore, three treatment groups of ten each for the males, and similarly three groups of females.

Each treatment group, it must be remembered, was composed of five animals of alcoholic ancestry and five whose ancestry was wholly free from alcohol. Hereafter, for simplicity, animals of alcoholic ancestry will be known as treated, and animals of control ancestry as controls, although in this experiment the so-called controls were tested for resistance in the fume tanks along with the treated.

These sixty rats were approximately the same age (average seventy-two days), there being at most only five days difference (usually less) between any treated rat and its corresponding control. There was a difference of less than one gram between the mean weight of the treated and control groups, as indicated by the following:

Control ♂♂ 200.00 ± 3.14 — Treated ♂♂ $199.28 \pm 2.20 = 0.72 \pm 3.84$
Control ♀♀ 172.50 ± 3.24 — Treated ♀♀ $171.53 \pm 2.30 = 0.97 \pm 3.76$

Any differences in resistance due to differences in age and size were therefore eliminated.

Alcohol fumes were administered by means of airtight fume tanks of galvanized iron, measuring externally 24″ x 12″ x 12″. Saturation of the fume tanks was obtained by spraying 150 cc of ethyl alcohol (95 per cent.) over the walls and floor, allowing the alcohol to evaporate over night. Ten males, five control, five treated, were placed in one fume tank, and ten females, five control, five treated, in another. The front walls of the tanks were plate glass so that the animals could be observed during treatment. Animals of the two groups were placed in the fumes at the same time and were not removed until they were unable to stand, and all voluntary movement had ceased. The length of time it took each rat to reach the condition of complete narcotization was the indicator of its power of resistance. Each rat upon removal from the fume tank was identified by a number in the ear, and the time spent in the tank recorded to the nearest minute. Control and treated animals were indistinguishable during treatment, and it was not until the rats were removed individually and their numbers recorded that they were identified as belonging to control or treated lines. The determination of the degree of anesthetization was made by the same person throughout the experiment, so that the personal equation was reduced to a minimum. Treatment was given daily on five consecutive days.

Results

Analysis of the data has been by biometrical methods. Calculations have been made of mean time, standard deviation and coefficients of variation with their probable errors. Each of these constants will be discussed separately.

Table 1 shows the mean average treatment time in minutes for the males and females of groups 1, 2 and 3, combined. Column 4 gives the differences between the control and treated animals with their probable errors, and the last column (to the right) each difference divided by its probable error. In no case is the difference statis-

TABLE I

A TABLE SHOWING THE MEAN AVERAGE TIME OF TREATMENT IN MINUTES FOR THE CONTROL AND TREATED RATS OF GROUPS 1, 2 AND 3, COMBINED

Males

Day of treatment	Control	Treated	Difference + tests gr. — tests less	Diff/P.E.
1	79.33 ± 3.12	74.00 ± 2.14	— 5.33 ± 3.78	1.41
2	74.00 ± 2.83	67.14 ± 2.40	— 6.86 ± 3.56	1.92
3	76.66 ± 2.43	72.66 ± 2.41	— 4.00 ± 3.57	1.12
4	84.00 ± 1.99	82.28 ± 2.17	— 1.72 ± 2.58	.....
5	78.00 ± 1.93	75.71 ± 1.89	— 2.29 ± 2.70	.....
Total 5 day treatment	78.26 ± 1.17	74.22 ± 1.13	— 4.04 ± 1.62	2.49

Females

1	104.00 ± 1.99	94.66 ± 2.11	— 9.34 ± 3.89	2.39
2	86.00 ± 1.89	88.00 ± 1.87	+ 2.00 ± 3.58	.....
3	92.00 ± 1.83	83.33 ± 2.67	— 8.67 ± 3.23	2.68
4	93.08 ± 1.73	85.72 ± 2.26	— 7.36 ± 2.84	2.59
5	86.66 ± 1.21	84.61 ± 1.59	— 2.05 ± 1.98	1.03
Total 5 day treatment	92.57 ± 1.24	87.18 ± 1.13	— 5.39 ± 1.87	2.82

tically significant (*e. g.*, three times its probable error), and in three cases the probable error is greater than the difference. A study of these differences also reveals that in all except one (second day's treatment for females) the difference is in favor of the controls. That is to say, the controls have an *actually* greater resistance to the fumes than do the treated, although as shown in Table 1 the differences are not significant. Figure 1 is a graphic representation of the means given in Table 1.

The means of the individual groups (Table 2), when the results of all five days' treatment are taken together, are consistent with those of the combined groups. Here again the differences are not significant, and of six groups, the actual differences of two only are in favor of the treated, while four are in favor of the controls.

Coming to the mean time of the individual groups for daily treatments, the situation is this: A survey of Table

TABLE II

A TABLE SHOWING THE MEAN TIME OF FIVE DAYS' TREATMENT IN MINUTES FOR THE CONTROL AND TREATED ANIMALS OF INDIVIDUAL GROUPS

Group No.	Control	Treated	Difference + tests gr. — tests less	Diff/P.E.
		Males		
1	80.40 ± 1.49	76.00 ± 1.27	— 4.40 ± 1.96	2.24
2	83.20 ± 1.46	84.00 ± 1.75	+ 0.80 ± 2.27	.....
3	71.20 ± 2.29	63.33 ± 1.38	— 7.87 ± 3.84	2.06
		Females		
1	89.50 ± 1.08	92.27 ± 0.86	+ 2.77 ± 1.66	1.66
2	95.60 ± 1.52	93.60 ± 1.36	— 2.00 ± 2.05	.....
3	92.00 ± 2.05	85.83 ± 1.72	— 6.17 ± 2.68	2.30

3 shows that twenty-six of thirty of the differences are in favor of the controls, and six of the twenty-six are significant differences. While the number of significant

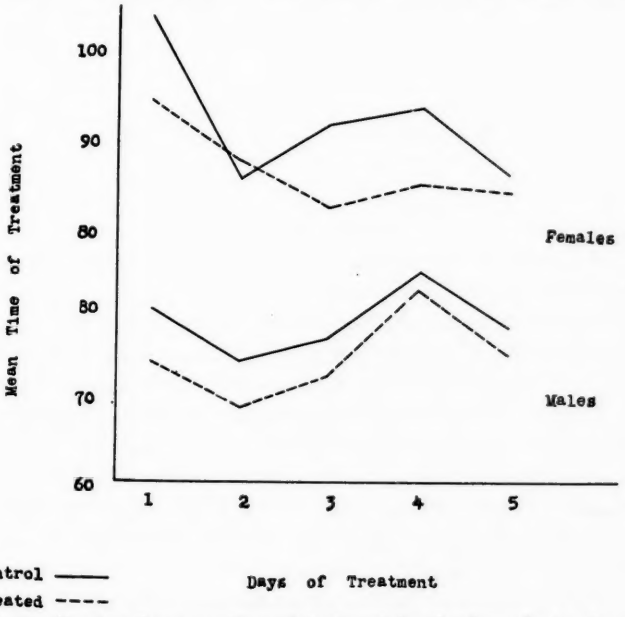

FIG. 1. Showing the mean time of treatment for the descendants of control and treated animals of groups 1, 2 and 3, combined.

TABLE III

A TABLE SHOWING THE DIFFERENCES IN MINUTES BETWEEN THE MEAN TIME OF DAILY TREATMENTS OF THE CONTROL AND TREATED ANIMALS OF GROUPS 1, 2 AND 3

Day of Treatment	Difference Males + tests gr. — tests less	Diff./P.E.	Difference Females + tests gr. — tests less	Diff./P.E.
		Group 1		
1	— 0.00 ± 3.84	.....	— 2.00 ± 4.26	.....
2	—16.00 ± 5.99	2.67	+12.00 ± 4.68	2.56
3	— 0.00 ± 0.00	.....	+ 1.50 ± 4.56	.....
4	— 8.00 ± 3.81	2.09	+ 1.50 ± 3.76	.....
5	— 6.00 ± 5.31	1.12	— 0.00 ± 0.00	.....
		Group 2		
1	— 2.00 ± 4.67	.....	— 0.00 ± 3.29	.....
2	— 0.00 ± 3.91	.....	— 2.00 ± 4.82	.....
3	— 6.00 ± 2.62	2.29	—14.00 ± 3.52	3.97
4	+12.00 ± 5.90	2.03	—14.50 ± 3.92	3.95
5	— 0.00 ± 0.00	.....	— 0.00 ± 3.30	.....
		Group 3		
1	—12.00 ± 6.85	1.75	—22.00 ± 5.66	3.88
2	— 9.00 ± 4.90	1.83	— 4.00 ± 4.26	.....
3	— 7.50 ± 4.36	1.72	—22.00 ± 6.36	3.45
4	—26.00 ± 5.77	4.50	—12.00 ± 4.37	2.74
5	— 1.00 ± 3.50	.....	—26.00 ± 5.72	4.54

differences is not large, some weight should be given to the consistency of the data.

Should it be conceded that the differences in general significantly favor the controls, the inheritance of resistance to alcohol, as indicated by this experiment, is still negative. For, if the descendants of treated animals had inherited a resistance to alcohol from their parents, one would expect them to be able to withstand the fumes for a longer period of time. On the average just the reverse was true, since the majority of the differences are in favor of the control descendants. The slightly greater resistance on the part of the controls, observed in this experiment, can not be attributed to a greater vigor, since

the two groups have been shown to be equally vigorous and of approximately equal weight and age.

TABLE IV

A Table showing the Coefficients of Variation for the Control and Treated Animals of Groups 1, 2 and 3, Combined

Males

Day of treatment	Control	Treated	Difference + tests gr. — tests less	Diff/P.E.
1	22.55 ± 2.77	16.58 ± 2.04	— 5.97 ± 3.43	1.74
2	21.95 ± 2.70	19.84 ± 2.53	— 2.11 ± 3.69	.....
3	18.23 ± 2.24	17.68 ± 2.17	— 1.55 ± 3.11	.....
4	13.60 ± 1.60	14.64 ± 1.86	+ 1.04 ± 2.45	.....
5	14.19 ± 1.74	13.86 ± 1.76	— 0.33 ± 2.47	.....
Total 5 day treatment	19.18 ± 1.43	19.00 ± 1.03	— 0.18 ± 1.76	.....
		Females		
1	10.99 ± 1.35	12.77 ± 1.53	+ 1.78 ± 2.06	.....
2	12.46 + 1.53	12.20 ± 1.50	— 0.26 ± 2.14	.....
3	11.36 ± 1.39	15.37 ± 2.42	+ 4.01 ± 2.55	1.56
4	10.69 ± 1.33	13.04 ± 1.66	+ 2.35 ± 2.12	1.10
5	7.19 ± 0.99	9.95 ± 1.31	+ 2.76 ± 1.64	1.68
Total 5 day treatment	12.86 ± 1.45	14.88 ± 1.37	+ 2.02 ± 1.94	1.04

Table 4 shows the coefficients of variation for the total control and treated animals of groups 1, 2 and 3. Variation constants, *e.g.*, standard deviation and coefficients of variation, were also computed for the separate groups. The differences in no case are significant and in many instances are several times less than their probable errors. In order not to extend the paper unduly, Table 4 is given as representative of these variation constants, which are consistently the same throughout the groups.

The relative variability of the control and treated animals is strikingly constant. The descendants of controls do not tend to deviate more from the average period of endurance than do the descendants of treated. If the treated rats have any advantage of inherited resistance, one would expect them to react more consistently and

with less deviation from the average time than the controls. Such was not the case, there being no significant differences between the variation constants of the two groups. It is certain that the general health of all the animals was kept as nearly constant as possible, and the individual variation observed seems to be purely at random, as would be expected from any group of animals, regardless of ancestry.

SUMMARY OF EXPERIMENTAL RESULTS

An experimental test of the resistance of two groups of rats, one having ten generations of alcoholic ancestry and one having entirely non-alcoholic ancestry, shows that no increased resistance to alcohol acquired by individuals during their lifetime is in any degree passed on to their progeny. The slight differences observed between the two groups are for the most part in favor of the controls. The rats vary individually in a manner quite in accordance with that which might be expected, had they been chosen at random, without regard to ancestry. There were no cumulative effects of ten generations of acquired resistance, and no inheritance, for the individuals of each succeeding generation reacquired the resistance as their parents and grandparents had done before them.

ALCOHOL AND THE INHERITANCE OF ACQUIRED CHARACTERS

It has been shown by this experiment that acquired resistance to alcohol is not inherited. Redfield ('25) has discussed the bearing of the alcohol work upon Lamarck's theory of evolution. He uses MacDowell's paper ('22) to give point to his criticism of the work, which is, in brief, that the one aspect of the alcohol work having any bearing on the inheritance of acquired characters has been entirely overlooked, namely, an increased resistance to alcohol fumes. It was apparently Redfield's idea that the increased resistance to alcohol acquired by each generation would be transmitted, and that such transmission would constitute the inheritance of an acquired modification.

Stockard and Papanicolaou ('18) have reported that in alcoholized guinea pigs the untreated offspring of treated animals were defective. The animals were inferior to controls in fertility and in the quality of the offspring produced. This condition the authors attribute to injuries inflicted upon the germ cells, as shown by the fact that offspring from treated parents, although themselves not treated, produced equally or more defective young than treated animals. In this manner, they say, the defects and degenerate conditions were passed on to subsequent generations.

Pearl ('17), repeating Stockard's experiments with chickens, secured results which were exactly opposite, finding that in each of eight points considered the offspring of treated parents, either one or both, were superior. This Pearl explains on the basis of selection. The treatment, he holds, acts as a selective agent upon the germ cells, entirely eliminating from zygote formation the weaker and less vigorous, and the gametes which survive this selective process and take part in zygote formation are the most vigorous and resistant part of the germ cell population.

As is pointed out by Pearl ('24), Stockard's earlier work emphasized only the production of defects and their transmission. In his later work (Stockard '22) he accepts the results of Pearl in all essential particulars and admits the action of alcohol as a selective agent. The weakest cells, he says, have been eliminated, while the slightly more resistant survive to zygote formation, but the gametes formed are so defective that many die before birth. Others, still more resistant, survive to birth but are defective. Many of these defectives die early in postnatal life. Those which live to produce the next generation have in turn defective offspring without treatment, because "weak cells give rise to other weak cells." This latest interpretation is, of course, in agreement with the work of Pearl.

The results of Hanson (previously cited), based on ten generations of treated animals and their controls, are

also in accord with Pearl's interpretation. It seems evident that none of the experiments with alcohol, thus far presented, gives any indication that alcohol has produced a specific alteration of germ plasm, as would be demanded had an acquired character been transmitted.

CONCLUSION

Increased resistance to alcohol fumes is a physiological character. As such it is built up gradually within the system, involving complex chemical changes. Most of the studies which have been made of the inheritance of acquired modifications have been directed toward strictly morphological characters. In answering the criticisms of those who deny the inheritance of acquired characters, some present-day Lamarckians have called attention to this fact, stating that they do not claim that acquired morphological characters in themselves are evidence in favor of the Lamarckian point of view, but that a truly acquired character is one which involves the physiological reaction of the entire organism to some external agent. Increased resistance is just such a character, and, were it transmitted, would constitute an acquired character in the Lamarckian sense.

Since it has been shown by this experiment that acquired resistance is not inherited, the one aspect of the alcohol work which might have lent support to the Lamarckian hypothesis has been eliminated. Alcohol seems to act as a selective agent only, and produces no new, heritable variations. The alcohol work in general demonstrates this fact. The results of this experiment show neither the inheritance of acquired characters nor the selection of germ cells more resistant to alcohol, since descendants of control animals, never subjected to a selective process, possessed a slightly greater resistance. The difficulty of separating the inheritance of an acquired character from the operation of selection renders the alcohol work unreliable as a test of the Lamarckian hypothesis. Consequently, the experiments with alcohol,

thus far presented, throw no light upon the problem of the inheritance of acquired characters. Many of them, of course, were not designed to test the validity of the Lamarckian hypothesis, although this paper deals directly with the problem, and the results are negative.

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GENETIC EXPERIMENTS WITH POND SNAILS LYMNAEA AND PHYSA[1]

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THIS is one of three papers on the general problem of reproduction in hermaphroditic fresh-water snails. In the other two papers the writer maintains that the anatomy and functions of the reproductive system probably will not permit normal cross-fertilization to occur in mated individuals of *Lymnaea stagnalis appressa* Say (Crabb, '27a), and he has shown by cytological methods applied to virgin material that self-fertilization is the normal method of reproduction in isolated individuals of this snail (Crabb, '27b). Although the experimental work here set forth is limited to two genera of pond snails, the work of Brockmeier ('88) on isolated *Helix*, Braun ('88) on isolated *Lymnaea auricularia* and Cook ('95) on *L. auricularia* and *Arion ater* and that of other investigators indicates that self-fertilization may occur in both land and fresh-water hermaphroditic gastropods.

This problem was begun at the suggestion of Professor A. Franklin Shull and carried out under his direction. I wish to express my sincere thanks to Professor Shull for the interest he has taken in the work and for his helpful criticisms. I am indebted to Dr. Bryant Walker and Mr. W. J. Clench for having identified the individuals of the parent stock from which the different forms used in these experiments were obtained.

I. BREEDING EXPERIMENTS

It was hoped that breeding experiments would demonstrate the mode of reproduction in pond snails, for inheritance would be exclusively maternal in case of par-

[1] Contribution from the Zoological Laboratory of the University of Michigan.

thenogenesis, apparently maternal if self-fertilization occurs (in spite of mating), but biparental in case of cross-fertilization. Therefore diligent search was made for distinguishing characters among wild snails and individuals of mass and isolation cultures of *Lymnaea s. appressa, L. columella, L. palustris, Planorbis trivolvis, Planorbis campanulatus, Physa sayii* and *Physa gyrina,* and only six were found. For whatever interest they may have for the student of variation in snails these characters are here briefly described, although, as pointed out below, they afford no solution of the problem of reproduction because they are not inherited.

(1) Notched Shell in L. s. appressa

In a mass culture of about fifty half-grown snails fourteen were found which had deeply notched shells and were used in experiments. The notch was V-shaped and varied in position from the anterior to the lateral margin of the lip of the shell in different individuals. In some instances it attained a depth of more than a fourth of the body whorl, but in every instance it was obliterated in about six weeks by the deposition of normal shell tissue. However, the presence of the notch in immature snails was indicated when they were fully mature by one or more scar-lines in the shell.

(2) Prong-Tentacle in L. s. appressa

An adult wild snail having a projecting point on the medial side of the left tentacle is the mother of the individuals used in experiments.

(3) Bifurcated Tentacle in L. s. appressa

A wild snail having the right tentacle shortened and split lengthwise was used in experiments.

(4, 5) Coiled Egg-Mass and Black Penis in Physa gyrina

Two adult wild snails deposited some twenty masses of eggs, all of which were loosely coiled instead of being

reniform, as is characteristic of our *Physa*. In addition to laying coiled egg-masses one of these snails had a very dark ("black") copulatory organ.

(6) Prong-Tentacle in Physa gyrina

A wild individual having a prong on the medial side of the right tentacle near the tip used in experiments.

A brief review of the experiments to test the inheritance of these characters may be of further interest. The prong-tentacled *L. s. appressa* (2) was mated, as the male, with the one having a bifurcated tentacle (3). Since it is safe to assume that reciprocal copulation occurred before the death of the latter, individuals having the tentacle bifurcated were expected in the progeny of the prong-tentacled snail. Reciprocal copulation was observed between the two *Physa* which laid coiled egg-masses (4), and twelve subsequent eggs were isolated in finger-bowls and allowed to hatch. It is not known whether or not these eggs were deposited by the snail having the black penis (5). The virgins developed from these isolated eggs were designated *Physa gyrina byersi* and were used in the following breeding experiments: a *P. g. byersi* was reciprocally mated with a virgin *P. sayii;* then the individuals were isolated before ovipositing and the offspring of each reared separately. The parent *P. g. byersi* and all its progeny died, and only eleven F_1 of the *P. sayii* were obtained.

Another experiment using the same technique with different individuals of the same parent stock resulted in seventeen F_1 from *P. sayii* eggs, seven F_1 and five F_2 from the *P. g. byersi* eggs.

A *P. g. byersi* was reciprocally mated with a virgin *P. gyrina;* both parents and their respective progeny were kept separate. The *P. gyrina* progeny was carried to the third generation.

Each of the above genetical experiments was carried to the F_2 in mass cultures or to the F_1 or F_2 in isolation cultures, with the exception of the eleven F_1 of *P. sayii.*

Three hundred and forty-three individuals thus reared reached maturity, but did not show any of the distinguishing characters. However, in a mass of eggs deposited by the prong-tentacled *Physa gyrina* (6), an individual appeared in which this character was accompanied by a second character in the form of a prong on the medial side and near the base of the left tentacle. In the light of the genetical experiments mentioned above it appears that in all probability neither of these abnormal tentacles was transmitted by the mother. The genetic tests therefore failed to demonstrate the mode of reproduction in these snails.

Notwithstanding the fact that the genetical results show nothing of a definite nature, the presence of a prong-tentacled individual in laboratory reared stock is significant because it shows that contrary to the opinions of Brauer ('08) and others abnormal tentacles are not always the result of regeneration. However, several investigators have conducted regeneration experiments in which the tentacles of gastropods were variously mutilated with the result that the regenerated organ was usually abnormal. From these experiments they have concluded that abnormal tentacles are the result of mutilation, hence are not inherited. Brauer ('08) believes that this is true for *Helix, Lymnaea stagnalis* and *Planorbis corneus.* He appears to have performed no breeding experiments. Cerny ('07) found that *L. stagnalis, Planorbis corneus, Paludina vivipara* and *Limax arborum* regenerate tentacles, some of which are abnormal. Hanko ('12) collected 270 specimens of the prosobranchiate gastropod *Nassa mutabilis,* twenty-six of which possessed abnormal tentacles which he concludes are the result of incomplete regeneration. Megusar ('07) cut off the tentacles of *L. stagnalis* and found that they were often abnormal when regenerated.

Several observers have found many abnormal and bizarre forms of shells, some of which have been considered mutations. Stubbs ('98) found many fantastic

shells and some albino pond snails under circumstances of limited range, which caused him to consider them mutations. In the light of Crépède's work ('10) in which it was found that an infusorian subsists upon the ovotestis in *Helix,* causing the shell to assume most extraordinary form, this limited range probably suggests that parasites or some cause other than heredity probably produced Stubbs' "mutations." Diver ('25) found a number of abnormal shells in his cultures of *Lymnaea peregra,* and others have reported similar abnormalities. The writer found that a number of extrinsic conditions will cause the shell to develop abnormally.

II. RÉSUMÉ OF THE LITERATURE

A fairly thorough search through available literature shows that most of the work on genetics of gastropods falls into two classes of experiments; crosses between subspecies and inheritance of sinistrality in dextral forms.

(1) Hybridization

Chaster ('99) found *L. stagnalis* and *L. auricularia* copulating in a pond. The young of the *L. auricularia,* which functioned as a female, were killed when one year old and their shells carefully examined. These resembled neither parent but were "unmistakably *L. peregra.*" Hynemann ('69) mated *L. peregra* with *L. auricularia,* which functioned as female and subsequently laid two masses of eggs "which were not fertilized by this copulation." W. D. Lang ('07) twice observed a *L. peregra* pairing with a *Planorbis corneus* acting as female, but he gives no genetical data.

Of adult material collected in February, "before the period of copulation," Pelseneer ('19) mated *Limnaea glutinosa* × *L. auricularia; L. glutinosa* × *L. palustris; L. glutinosa* × *L. stagnalis; L. glutinosa* × *L. peregra; L. peregra* × *L. stagnalis; L. peregra* × *L. palustris; L. palustris* × *L. stagnalis; L. palustris* × *L. auricularia;*

and *L. auricularia* × *L. stagnalis*. Each pair copulated, and all acting females deposited masses of eggs. These masses, their contained eggs and the embryos and young snails which hatched from them conformed in every respect to the mother species. Pelseneer concluded that these "false hybrids" are produced without amphimixis, or by parthenogenesis induced by foreign sperms, or by diverse chemical substances. Therefore these are cases of "pseudogamy." Brockmeier ('08) thinks that he obtained *L. palustris* from *L. truncatula* eggs, but he is uncertain whether to attribute this to environment or to heredity.

There have been numerous attempts to hybridize land snails, and many instances of two species mating in nature have been reported. Among these some seem to have actually hybridized. I should mention that *Helix* and many other land snails cross reciprocally at one mating. Caziot ('07) lists several land snails observed mating with other species, but he doubts if "offspring resulted from any of these ill assorted unions." A. Lang ('08) conducted a series of crosses with *Helix nemoralis* and *H. hortensis* involving several morphological characters of the shell, different parts of the sex organs and color of the shell and certain fleshy parts, and found an intermediate development of the parental characters in the hybrids. In a later work ('14) he crossed a five-banded with a bandless *Tachaea* (*Helix*) *nemoralis* and got a definite 3:1 ratio with bandless dominant.

Although Lang's genetical experiments are the best known in the literature of genetics of Gastropoda they are open to serious objections. In view of the fact that *Helix hortensis* has been known to deposit viable eggs after having been kept in isolation two years, that *H. nemoralis* has been able to function thus after more than a year of isolation (Brockmeier, '88), and that isolated *Arion ater* have laid viable eggs (Cook, '95), one hesitates to accept Lang's ratios as being the result of his

experimental crosses. These "definite ratios" could hardly be obtained unless there were an interval during which the snails were rendered unisexual, for otherwise self-fertilization might occur. Such a condition of unisexuality during copulation has been described for *Helix arbustorum* by Buresch ('12) in which all the ripe spermatozoa are forced out of each snail's hermaphrodite apparatus and its male conduit into the "penis pocket" where they are formed into spermaphores; then the epithelial lining of part, if not all, of the hermaphrodite and female apparatus sloughs off just before copulation. Thus at the time of actual copulation each of the snails is rendered unisexual so far as self-fertilization is concerned. During copulation each injects its spermatophores into the sperm receptacle of the other, and cross-fertilization takes place.

Baltzer ('13) made a cytological investigation of the male cells of some of Lang's ('11) "Falsche Bastarde" *Tachea* (*Helix*) *hortensis* × *T. austriaca* and found that these "hybrids" had twenty-two or twenty-three chromosomes. Since this number was found in *T. hortensis* and twenty-five in *T. austriaca* he concluded that the "hybrids" were merely the parthenogenetic or self-fertilized offspring of *T. hortensis*. Lang ('11) points out that these were "false hybrids" because they resembled the mother more than the father. Hofmann ('12) describes several pathological and other abnormal modifications in Helix, such as paired male organs, missing parts of male and of female organs, fused tentacles, etc. Although there is nothing in his experimental work or his review of fifteen other articles to show whether any of these abnormalities are inherited, it raises the question whether some of the variations which Lang ('08) obtained might not be purely ontogenetic. Darbishire ('05) raises another point of objection to Lang's earlier work (1904 which is summarized in '08) on snails. He says:

> The way in which Lang's data were collected does not admit of their description in terms of the law of ancestral heredity. . . . Dark-lipped *H. hortensis* are not rare, and pale-lipped *H. nemoralis* are occasionally found. (Pearson also holds this view, Biometrica, II, p. 211.)

Pelseneer ('19) thinks that Lang's snails failed to hybridize, even though copulation occurred.

Stelfox ('15) crossed *Helix aspersa* and *H. exalbida* and in the second generation obtained seventy-two white and 239 brown individuals. He concludes that "varieties are hereditary, size and texture of a shell can be influenced by food supply, and its general environment." Honigmann ('08) raised numbers of albino *Lymnaea stagnalis bungei* and found that albinism remained to the third and fourth generation, therefore he concludes that this form has been established.

(2) Inverse Symmetry

The results obtained by Boycott and Diver ('25) have given the most promising outlook for the future of any serious genetical experiments with pond snails of any available work. These investigators reared broods from supposedly "cross-fertilized" and isolated ("single") cultures, and their results from dextral and sinistral "crosses" led Sturtevant ('23) to formulate the following explanation:

> An analysis of the data presented suggests that the case is a simple Mendelian one, with the dextral character dominant, but with the nature of a given individual determined, not by its own constitution, but by that of the unreduced egg from which it arose.

He also points out the possibilities of these ratios being merely fortuitous.

Wilson ('25), in commenting upon Boycott and Diver's paper and Sturtevant's analysis of it, says:

> With rare exceptions a particular individual, whether dextral or sinistral, produces only dextral or sinistral offspring in a brood . . . but not both types at once. This is made intelligible by the assumptions (1) that genetically the dextral type is dominant over the sinistral, but (2) that the character of a particular brood is due to the genetic constitution of the egg before maturation and fertilization.

Diver's later paper ('25) appears to contribute very little new in material to the problem in hand other than a large number of additional experiments and further elaboration upon the "suppression hypothesis." In their preliminary paper Boycott and Diver ('23) showed that "all the broods obtained could at once without doubt be placed in one of the six classes in accordance both with the appearance of the young snails contained in the broods, and the manner in which they are disposed in regard to other broods." These brood types as set forth by Diver ('25) are:

A	B	C	D
All dextral	3 dextral to 1 sinistral	1 dextral to 1 sinistral	All sinistral
	E	F	
	Mostly sinistral with a few odd dextrals	Mostly dextral with a few odd sinistrals	

All six types may be obtained from sinistral as well as from dextral parents.

Brood types E and F are supposed to be suppressed A and D types. Diver does not think that Sturtevant was justified in his analysis of Boycott and Diver's paper but does not offer a more suitable interpretation of the results.

Since inverse symmetry in the gastropods is a much discussed point, additional data from different sources are desirable. Crampton ('24) states that in the viviparous land-snail *Partula,* he (1916) and Mayor (1902) found only one type of young in the brood pouch of an individual; but in a later article ('24) he reports both dextral and sinistral young in the brood pouch. Of 1,317 instances in *Partula suturalis,* 1,133 instances were observed in which two or more young were like the parent; while 184 cases were observed in which two or more young were unlike the parent. From these observations he drew the following conclusions:

> The exceptional occurrence of mixed broods in *Limnaea* and *Partula* would indicate that the hereditary procedure postulated by Sturtevant is not invariable, and that there are unusual circumstances under which additional factors may operate so as to produce other than the expected results.

In a later article ('25) he presents additional data to confirm this view.

Conklin ('03a, '03b) maintains that the cause of inverse symmetry in gastropods is ontogenetic rather than phylogenetic. In the former he points out that inverse organization probably arises about the time of maturation or pre-fertilization of the egg:

> In dextral snails the polar bodies are formed at what was the free pole of the ovarian egg, and if the polar bodies were to be formed at the opposite or attached pole in sinistral forms it would entirely and satisfactorily explain their inverse symmetry. While such reversal of the polarity of the egg in sinistral forms has not been demonstrated, certain observations have been made which render it probable.

For a number of years Conklin tried to reverse the polarity of gastropod eggs, but in 1910 he came to the conclusion that it could not be accomplished by centrifugal force.

Hesse ('14) cites a number of references and concludes that "the offspring of sinistral *Helix* are without exception dextral." However, he cites Collin (1872), who collected twenty sinistral *Lymnaea stagnalis,* one of which he put in an aquarium and from it obtained sinistral young. Adams ('23) mated a dextral and a sinistral *Lymnaea peregra* and secured a number of masses of eggs. Two of them contained both dextral and sinistral young. From these observations he concludes that there is a possibility of biparental reproduction, but that probably most of the eggs deposited by these snails were self-fertilized. Thus it appears that the investigators have been unable to show whether or not sinistrality is a transmissible character in hermaphroditic snails.

III. Summary

(1) In an attempt to determine whether or not hermaphroditic fresh-water snails normally reproduce biparentally, individuals of *Lymnaea stagnalis appressa,*

Physa gyrina and *Physa sayii* exhibiting abnormalities which it was hoped would prove to be distinguishing characters were used in breeding experiments.

(2) Three hundred and forty-three F_1 and F_2 progeny reared in isolation and F_3 reared in mass cultures reached maturity or even old age without showing one of the expected characters. None of these characters was observed in immature progeny which died before attaining the size at which they would have been considered sexually mature.

(3) The only instance in all the cultures which suggested inheritance of any of the distinguishing characters was that of an F_1 *Physa gyrina* which had a prong on the medial side of its right tentacle near the tip, as had its mother, but it also had a prong on the medial side of the left tentacle near the base, which did not occur in the mother.

(4) In reviewing a considerable amount of the literature on heredity in Gastropoda it is shown that there is a very marked lack of agreement among the various investigators.

IV. Conclusions

Since in these cultures none of the distinguishing characters reappeared in any of the offspring resulting from self-fertilized or isolated parents, it is evident that the characters were not transmissible. The writer believes that the single instance cited in which a maternal character reappeared was merely fortuitous.

In general, the ratios obtained by other investigators who have mated pond snails can be interpreted only in terms of matroclinous inheritance, or as being merely fortuitous and probably resulting from non-hereditary causes.

The results of these experiments afford no solution of the problem of reproduction because none of the characters was definitely transmitted. Neither does the literature on this subject afford proof of the mode of repro-

duction in hermaphroditic land or fresh-water gastropods. However, numerous instances are cited in which self-fertilization is indicated.

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VARIABILITY AND RACIAL MIXTURE

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THE biometric method has come to lay great stress on the variability of populations as a major clue toward the solution of the problems of their development and in the discovery of the applicability of the findings of the geneticists to human populations. One of the hypotheses which has gone hand in hand with the use of the concept of variability is that where there is a greater variation in one of two populations, that which has the larger represents the greater amount of mixture. And when "mixture" is spoken of, the connotation is that of "racial mixture." The logical conclusion is that the "pure race" is that which shows the lowest variability, and that when large variation is found in a population, this means it is the result of a great amount of race-crossing.

We see that this assumption is a real one in the minds of biologists and biometricians when we consider some of the statements which have been recently made regarding the matter. Thus, in a paper published a short time ago, Castle remarks that ". . . as heterosis disappears, the population of later generations will be intermediate in character, and probably more variable than either uncrossed race."[1] Wissler, in a consideration of the subject of variability, remarks that "what we have . . . in a population unit is a number of types or pure lines, thrown together, each with its own range of variability, and these variabilities have a way of combining so as to increase the variability of the whole. . . . As is often said, the range of stature will be greater among mixed races. This is, in fact, a recognized law of biology."[2]

[1] W. E. Castle, "Biological and Social Consequences of Race Crossing," *Amer. Jour. Phys. Anthropology*, Vol. ix (1926), p. 152.

[2] Clark Wissler, "The Relation of Nature to Man in Aboriginal America," pp. 126–127.

These are sufficient to show the trend of thought regarding the usefulness of variation as an indication of the development of biological types, and what is regarded as its significance.

It seems, however, that the assumption that low variability is an index of racial purity has been made too freely. As has been said, this would seem to follow logically from the hypothesis which is usually held, and particularly in view of the general application of the Mendelian theory of the inheritance of unit characters which is advanced so often by geneticists and eugenists as being immediately applicable to human characteristics. For if there is mixture between populations having appreciably different physical characteristics, *i.e.*, different racial groups, then it would be expected that the offspring from such crosses would partake somewhat of the characteristics of each of the parental groups, by blending these characteristics, or, failing this, would revert to the types from which it came in the Mendelian ratio, more or less, increasing the variability of the mixed group when compared to that of either of the parental populations. Of course, if we define a race as a group which shows a low variability, then a population which is highly variable would, by definition, not be racially pure. But a race, as we conceive the term, does not explicitly comprehend the element of variability, rather being defined as a population which is marked by certain physical characteristics, taken more or less at random, and in which all the members of the race resemble each other more than they do the members of other races. The implicit assumption which has followed has merely carried the implication to its logical conclusion; if a racial group is marked by certain well-defined characteristics, then a population having them is not as variable as another having both them and the characteristics of another racial group with which it has mixed. Therefore, it is held that the "pure" population is less variable; and, therefore, from this it follows that low variability is an earnest of racial purity.

This point of view has not gone without challenge. Thus, Fischer[3] found in his investigation of the anthropometry of the Rehobother Bastaards, a group of Dutch-Hottentot crosses, that these people show an exceedingly low comparative variability in numerous traits. Sullivan,[4] working through Boas's Siouan material, showed that half-blood Sioux Indians are less variable than full-bloods in certain traits, and, presumably, than the white ancestry party to the cross. For example, in the cephalic index, the pure Sioux have a variability (represented by sigma) of 3.20, while that of the half-bloods is 2.54; in nasal height the pure Sioux vary to the extent of 3.94 mm, while the half-bloods vary only 3.55 mm; and so we might quote numerous other examples from this paper. Of course, the result is not always consistent, but in the majority of the traits measured the half-bloods are less variable than the full-bloods, or they have about the same variability. Further evidence is found in Wissler's working over[5] of Davenport and Love's anthropometric data gathered in the army during the late war, where it is found that while the Negro is most variable in stature and weight, in chest circumference he is the least variable among the nine national and racial elements of our population represented in the tables. Todd's work on the comparative structure of American Negroes and whites, made on cadavera material at Western Reserve University, has shown that his hybrid-Negro sample, in trait after trait, is less variable than the unmixed white.[6] For example, if we consider sitting height, we see that the unmixed whites vary to the extent of 3.41 cm, while the mixed Negroes have a variability of only 3.19 cm, while if we take length of the head as another example, the

[3] Eugen Fischer, "Die Rehobother Bastaards."

[4] Louis R. Sullivan, "Anthropometry of the Siouan Tribes," Anthrop. Papers, Amer. Mus. Nat. History, xxiii, III (1920), pp. 81–174.

[5] Clark Wissler, "Distribution of Stature in the United States," *Scientific Monthly*, xviii (1924), pp. 129–143.

[6] The results given here are not as yet published, but were furnished me through the kindness of Professor Todd.

variability of the white sample is 7.52 mm, while that of the Negro cadavera is 6.08 mm. Again, this is not the case in every trait, but it is found to occur in enough of them to give food for thought on the subject.

For these are not results such as would be expected to follow, if the hypothesis of variability as an index of racial purity were tenable. Why should the half-breed Indian be less variable in so many traits than his full-blooded brother? Or the Bastaard less variable than his Hottentot, or his Dutch, ancestry? These questions are the more interesting in the light of certain results which have come out of research which I have been conducting for the past three years on the variability of our Negro-white mixed population in this country—results which have direct bearing on the problem under discussion, and which strongly tend to corroborate the findings of the students whose work I have just mentioned—men who also have worked with populations of known racial mixture.

The investigation on which I have been engaged has included the measuring of American Negroes in New York City and at Howard University in Washington, D. C.[7] In New York there were measured about one thousand three hundred Negro children in Public School 89, Manhattan, and sixty-two male adult Negroes, while at Howard University there were measured four hundred and seventy-seven male students, all adults. The results, which are presented here, are drawn largely from the latter series, which is highly representative of the entire country, representing, as it does, every state where there are Negroes in any numbers, as well as other states where they are not so numerous. That the series is adequate

[7] This research was carried on under a fellowship appointment of the Board in the Biological Sciences, National Research Council, and the work in Washington was assisted by a special grant from the Committee on Human Migrations of the National Research Council. To the President and Faculty of Howard University for the cordial cooperation they extended to me, and to Dr. Jacob M. Ross, Principal of Public School 89, and his staff, for their forebearance and aid while I was working there, I owe my deep gratitude.

is to be seen if the results for the same traits are compared with those obtained by Davenport and Love for their series of about six thousand adult male Negroes measured in the army during the late war,[8] with which the results obtained by me check to a gratifying extent. And this research into the problem of variability under racial crossing has yielded results which, as has been remarked, tend to throw further light on the puzzling problem which is presented by the phenomena of variability in mixed and unmixed populations.

Fundamentally, the problem which presented itself to me was this: The American Negro represents a vast amount of racial crossing. To what extent, then, has this crossing affected the variability of the Negro population in this country? A genealogical investigation, which was carried on along with the measuring of the men, showed that the Negroes who live here represent much more mixture than has been generally thought to be the case. For, indeed, to a very appreciable extent they are a three-way rather than the two-way cross they are ordinarily held to be, for while 80 per cent. of the men measured by me claimed to be of other than pure Negro stock, one third of the total number knew of partial American Indian ancestry. All this causes the problem to lie in a field richer for research into this particular question and more provocative from the point of view of its theoretical aspects. For with this greatly mixed group, then, the problem poses itself as to whether this hybrid population is to be found to be homogeneous or heterogeneous and whether the large amount of racial crossing it represents has tended to increase greatly the variability of the resulting offspring.

As a step toward the solution of this problem there have been gathered comparative averages and variabilities of such populations for which these may be available, and for the same traits as those measured by me, to the

[8] Charles B. Davenport and Albert G. Love, "The Medical Department of the United States in the World War," Vol. XV, "Statistics"; part 1, "Army Anthropology," Washington, 1921.

extent to which these may be obtained. After a comparison of the averages and variabilities of the American Negro population which was measured in this study with these American Indian, European and African averages and variabilities, the first thing which strikes us is that, in the case of all traits for which there is a reasonably long series of means for these populations to which the hybrid Negro-white-Indian population measured by me is presumably related, the mean for the latter series lies between the averages of the other populations. Of course, this may be held to be somewhat aside from the point, since it is variation, and not average values, with which we are primarily concerned here. However, the point has real bearing on the argument, in that the thesis of a large variability for a mixed population is usually linked with that which holds that, in crossing, there is a segregation of traits toward one or the other of the parental types in the crossed offspring. This, however, is not the case where the American Negro is considered, and can be readily seen if the tables given below are consulted. The tables do not represent all the available data by any means. There are numerous populations for which data are available for the traits mentioned below, and there were thirty traits which I measured on each individual in the course in the investigation. For all this material there is not the space here, nor is its full presentation necessary to make the point, since the averages and variabilities given are adequately representative of the full data. Certainly, comparing the means given above, which are representative, as has been said, of the thirty tables of averages, one can see no indication of segregation toward the averages of the parent populations. However, this is but a point in passing, and I do not mean to argue that a genetical problem of the delicacy of this one can be solved by methods as rough as the one employed here. The data are merely given for whatever they may suggest to the reader.

COMPARATIVE AVERAGES AND VARIABILITIES OF AMERICAN NEGRO AND OTHER POPULATIONS

Table I. Cephalic Index

No. of Cases	Population	Average	Variability ($\pm\sigma$)
167	W. R. U. White Skulls	79.67	4.74
126	Delaware Indians	79.80	3.50
539	*Mixed Negroes*	*77.05*	*3.49*
19	Ekoi (West Africa)	75.26	3.27
55	Kajiji (West Africa)	75.17	3.07
727	Old Americans	77.95	3.01
40	Vai (West Africa)	76.05	2.96

Table II. Total Facial Height (mm.)

No. of Cases	Population	Average	Variability ($\pm\sigma$)
2,348	English criminals	123.73	7.70
72	Kagoro (West Africa)	112.04	7.52
20	Ekoi (West Africa)	114.45	6.82
247	Old Americans	119.30	6.72
537	Pure Sioux	124.60	6.37
534	*Mixed Negroes*	*122.60*	*6.31*
40	Vai (West Africa)	106.78	5.84

Table III. Height of Nose (mm.)

No. of Cases	Population	Average	Variability ($\pm\sigma$)
72	Kagoro (West Africa)	47.93	4.01
539	Pure Sioux	58.30	3.94
55	Kajiji (West Africa)	49.22	3.84
77	Mixed Sioux	54.90	3.55
247	Old Americans	53.50	3.36
539	*Mixed Negroes*	*53.57*	*3.35*
20	Ekoi (West Africa)	47.05	2.76
48	Ashanti (West Africa)	45.17	2.48

Table IV. Height of Ear (mm.)

No. of Cases	Population	Average	Variability ($\pm\sigma$)
84	Marquesans	67.10	5.72
247	Old Americans	66.90	5.72
2,338	English criminals	64.31	4.88
537	*Mixed Negroes*	*60.19*	*4.03*
20	Ekoi (West Africa)	59.55	3.96

Table V. Height Sitting (cm.)

No. of Cases	Population	Average	Variability ($\pm\sigma$)
30	Kajiji (West Africa)	84.44	3.94
96,239	White U. S. Troops	90.39	3.51
538	Pure Sioux	88.59	3.50
100	W. R. U. White cadavera	88.60	3.41
100	W. R. U. Negro cadavera	88.60	3.19
476	*Mixed Negroes*	*88.19*	*3.19*
19	Ekoi (West Africa)	85.97	3.07
37	Kagoro (West Africa)	86.51	3.00

Table VI. Stature (cm.)

No. of Cases	Population	Average	Variability ($\pm\sigma$)
30	Kajiji (West Africa)	168.30	8.57
96,596	White U. S. Troops	171.97	6.66
1,000	Cambridge (Eng.) Men	174.88	6.46
475	*Mixed Negroes*	*171.06*	*6.39*
20	Ekoi (West Africa)	166.86	5.83
727	Old Americans	174.30	5.80
47	Ashanti (West Africa)	164.21	5.53

We do, however, come to something quite decisive if we consider the second column in each of the above tables, the one which gives that of the variabilities. Noting the variabilities first for the unmixed European and African populations for which the data are given above, and then those of the mixed series of American Negroes measured in the course of this study, who are presumably descended from ancestry composed of the other populations or populations of the same general racial stock, one gets an interesting view of the situation and a confirmation of one's doubt that low variability is only found where racial purity occurs, or is an earnest of it. For no one would claim, even *a priori,* that the sample of American Negroes studied here is racially pure. Indeed, as has been remarked, it is as mixed a population as almost any conceivable can be—a three-way mixture of African, European and American Indian. And yet, if we consider these tables, we find that the lowness of the variabilities of the mixed American Negroes is remarkable in the light of the theory that high variation goes with large amounts of racial mixture.

Of the thirty traits measured, there are twenty for which enough comparative variabilities could be found in the literature to allow of a reasonable amount of comparison. Of these twenty traits, the sample measured in this study is least variable in eleven of them, while it is most variable in only four, leaving five traits in which it is about at the center of the list of variabilities. But the group which has this surprisingly low variability when compared to other (unmixed) populations is itself the

result of tremendous racial mixture. This seems to point to the fact that if variability is an indication of anything —as it does not seem illogical to suppose it must be—it is not an earnest of racial purity. And it points this strikingly; the results, as shown, do not seem to allow of equivocation. There is, apparently, no such association, and it is something other than racial purity which makes for a low variability. I do not mean, of course, that low variability can not be found in an unmixed racial stock. The Old American population measured by Hrdlička is composed principally of persons of unmixed Scottish and English origin and has a very low variability, as is the case with such a population as the Ekoi of West Africa, who are unmixed Negroes. But even in the case of these populations, it is to be noted that their variability is but little, if any, lower than that of the sample of mixed American Negroes considered here.

However, there is available further evidence looking toward the same conclusion which was uncovered in the course of this research. In working up the material, the data were divided into eight groups according to the genealogical statements of the men measured. These were: unmixed Negro, more Negro than white, about the same amounts of white and Negro, and more white than Negro, with, and also without, Indian ancestry for each class. The thirty traits were then studied within each of the eight classes, and the averages and variabilities of these distributions computed. Of course, there will be objections that taking the genealogical statements of the men measured at their face value is a hazardous step, and one which would tend to jeopardize any results which came from them. But I can only say that the analysis shows that the genealogies are quite valid in the sense that the different groups vary from Negroid to non-Negroid characteristics regularly and consistently, as they would have to do if they were actually of the amounts of crossing their members said they were. Therefore, we may dismiss this point without further discussion.

If we consider the variabilities of the genealogical groups, it would be expected that the unmixed Negro group would be the least variable if the hypothesis that low variability is a correlate of racial purity holds. But this group is found to have the lowest variability of the eight groups of varying amounts of mixture in only three out of the thirty traits measured. Another test can be applied. We can add the variabilities of each of the classes for the entire thirty traits, and see how the resulting sums rank. And we find that the lowest is not the unmixed Negro, but the group which includes those men who gave themselves as having more Negro than white blood, with Indian mixture in addition. The unmixed Negro class follows this and is almost identical with one of the mixed classes which has but a slightly higher summated variability. Again, this is not a result commensurate with the hypothesis generally held.

The question may then be fairly posed: What is the significance of low variability? If variability is not an indication of the racial purity or mixture of a population, what is its value in anthropometric studies? The answer is to be sought in a study of those groups in which low variability is found. The Tennessee mountaineers and the Bastaards, one group racially pure and the other of great mixture, both have it. The Old White Americans and the American Negroes both have it. A chance sample of white Americans, such as comprise Todd's white dissecting room population, do not have it, but the variabilities of the traits measured on them are high. The answer, it is believed, is fundamental to the biometric method and its concepts, and it is this: That the problem to be solved is not to be thought of in terms of the races to which a population studied may or may not belong, nor the extent to which it is a "pure" or a "mixed" racial stock. It is rather to be asked, in a study of contemporary human populations, whether a given group is homogeneous or heterogeneous in type (type here meaning a large number of physical characteristics), what has been

the historical connections which have made it what it is and the way in which it has historically developed, if this is possible to determine, from the parental types from which it has sprung. In the final analysis, it seems to me, the attempt to place populations blindly in racial categories seems a nullification of the effort involved, when the amount of mixture all existing populations represent is taken into consideration. Of course, one may attempt to catalogue a population as belonging to the major human groups, that is, as White or Negro or Mongol. Hooton has recently attempted an interesting methodological device for the determination of racial affiliations of populations studied.[9] But this, it seems to me, is of more importance when applied to skeletal series than when it is utilized for series of measurements on the living.

That the American Negro population, mixed as it is to such a very large degree, can be intelligently regarded as a homogeneous group is the conclusion which seems to follow the results of this investigation. And while it seems hopeless to do anything, biometrically speaking, with such a mixed population as this if racial affinities are held firmly in mind, the situation becomes at once clarified if the student is thinking in terms of homogeneity or heterogeneity of the population he is studying. It may not be amiss to show how the evidence has piled on evidence to establish the homogeneity of the American Negroes I have dealt with, in spite of the fact that they are so racially mixed. In the first study made of American Negroes,[10] one of the growth of Negro boys as compared to white boys, it was found that while the growth of Negro children is accelerated and that they are taller and heavier than white boys of like age, the variabilities for the two groups, taken age by age, are no greater for

[9] Its working out is best illustrated in Dr. Hooton's "The Ancient Inhabitants of the Canary Islands," Vol. VII, in the Harvard African Studies.

[10] M. J. Herskovits, "Some Observations on the Growth of Colored Boys," *Am. Jour. Phys. Anthropology*, VII (1924), pp. 439–446.

the mixed Negro boys than they are for the white. Next came a study of the variability of the family lines of the New York City mixed Negro population, as represented by fraternities of the Negro families which had children in Public School 89.[11] A low figure for the variability of family lines shows that there is homogeneity in the population, and it was not without something of surprise that it was found that the investigation had shown as low a figure for the variability of the family lines of the New York City mixed Negro population as that which has been found for the Tennessee mountaineers,[12] an inbred population of great racial purity, while both of these ranked very low when compared further with the variability of the family strains of a number of other populations for which this was computed by Boas.[13] The result from the computation, in which head-form was the trait used, was further corroborated by computation of the same formulae for the same group, but utilizing other traits.[14] The mechanism which made for this homogeneity and the fact that it actually exists in the American Negro population, was suspected at this time, but it was not until the adult series discussed in this paper was measured that the conviction was reached that in spite of the vast amount of racial crossing represented by the American Negro, he is really consolidating into a homogeneous population type, through a mechanism of social selection.[15] This discussion can be seen where referred to, but it can be said here briefly that it consists in a strong

[11] M. J. Herskovits, "On the Negro-White Population of New York City." . . . Proceedings, XXI^{e} Congrès International des Américanistes. The Hague, 1924. pp. 5–12.

[12] Isabel Gordon, "Reduction of Variability in an Inbred Population." MS (Doctoral Dissertation, Columbia University, 1925).

[13] Franz Boas, "On the Variety of Lines of Descent represented in a Population." *Amer. Anth.* (N.S.), XVIII (1916), pp. 1–9.

[14] M. J. Herskovits, "A Further Discussion of the Variability of Family Strains in the Negro-White Population of New York City," *Jour. Amer. Statistical Ass'n.* (n. s.), XX (1925), pp. 380–89.

[15] M. J. Herskovits, "The Color Line," *American Mercury,* VI (1925), pp. 204–208.

tendency for light-colored women to marry dark men, while pressure against mixture with whites operative within the Negro community prevents further infusion of white blood.

Thus it can be seen that the significance of variability in biometric studies has little reference, *per se,* to the problem of racial purity of a population. What it signifies is the extent to which a population may be thought of as a homogeneous unit or a heterogeneous one. The heterogeneity may come from the mixture of individuals of very different races, or it may come from the mixture of those of the same race, as, *e.g.,* Todd's results of large variability found in his unmixed white dissecting room population. Wissler found comparable results,[16] where he showed that the variabilities for the sections of this country known to be extremely homogeneous in type were relatively low (using chest circumference and stature as his measurements), while those for large cities, where types of all sorts mingle, were materially greater. Again, Boas's study[17] of Italian head-form material showed that where mixture between short- and long-headed Italians was occurring (in central Italy), the variability was considerably higher than in either the extreme north or the extreme south, where there is a preponderance of the one and the other type of head-form, respectively. Here there is no question at all of racial mixture, but merely the problem of the effect of mixture between two kinds of a certain trait on the resulting crossed population. In this case, the high variabilities showed that the mixture was still occurring, but it is quite natural to assume that were the population of Central Italy to remain isolated for a few generations, the variability would be found to be materially lower than it is at present under the continuing mixture of head-form types. We find that

[16] Clark Wissler, "Distribution of Stature in the United States," *Scientific Monthly,* XVIII (1924), p. 138.

[17] Franz Boas, "The Head-forms of the Italians as influenced by Environment and Heredity," *Amer. Anthropologist,* (n.s.), XV (1913), pp. 163–188.

the mixed populations of isolated valleys consolidate their physical form to a uniform type—and we find this same phenomenon in the process of occurring among the American Negro population, which has, for the past few generations, not been mixing with the white population, but breeding within itself.

Using this population as a further test, therefore, of the theory that low variability is an earnest of the amount of race mixture which is to be found in a population, we have seen that the expected results do not follow at all. But if we make our consideration on the basis of the extent to which the population is homogeneous or heterogeneous, we see that this one has become homogeneous to an appreciable degree, and, despite its being racially mixed to an enormous extent, that it displays a variability as low or sometimes even lower than its racially unmixed ancestral stocks. We may conclude, then, that if inbreeding in a mixed population occurs, variability need not be high merely because there has been mixture, but that high variation is to be expected in populations in which the type is heterogeneous, while, conversely, low variability occurs in any population, racially mixed or pure, which has, by breeding within itself, established a homogeneous type.

SHORTER ARTICLES AND DISCUSSION

THE EXPERIMENTAL PRODUCTION OF MELANISM IN LEPIDOPTERA

It has been remarked for some years by British naturalists (see Bateson, 1913) that in many species of Lepidoptera, especially Geometridae, melanic varieties have apparently come into existence within the past fifty years, and have in some cases more or less completely replaced the older, lighter type in certain districts of England and the Continent. Where genetic tests have been applied, the melanic form has generally been found to differ from the light type by a single Mendelian factor, which is in some species dominant, in others recessive or nearly so. This appearance and spread of melanic Lepidoptera has aroused the interest of many biologists, as being one of the very few recognizable cases of evolutionary change occurring in nature at the present time. In 1900 the Evolution Committee of the Royal Society instituted a collective inquiry into the phenomenon (Doncaster, 1906). Every investigator who has studied the problem seems to be convinced that this change is correlated with the industrialization of the districts affected. Bateson (1913) concludes: "Taking the evidence as a whole, we may say that it fairly suggests the existence of some connection between modern urban developments and the appearance and rise of the melanic varieties."

Accepting this correlation as a fact, the causal relation between industrialism and Lepidopteran melanism becomes an interesting, and perhaps profitable, problem in the mechanism of evolution. Among the factors which have been suggested are natural selection, Lamarckism and the direct induction of mutation by some substance or substances in coal smoke. Bateson (1913) concludes that natural selection, at least in the sense of protective coloration, can hardly be an effective factor. Harrison (1920), who has studied the whole subject very extensively, reaches the same conclusion, and favors the hypothesis of direct induction of mutation by chemical factors.

The recently published results of extended and careful experiments by Harrison and Garrett (1926) furnish strong evidence in favor of this hypothesis. Unfortunately, the authors, in the discussion of their results, confuse the issue by suggesting a "Lamarckian" interpretation. As this work is likely to be widely quoted as evidence in favor of Lamarckism, it may be

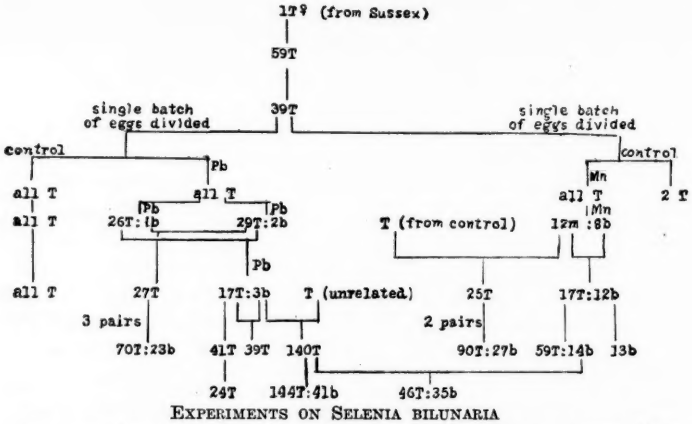
worth while to point out that the experimental facts, as stated by these authors, have no bearing at all on this question, whatever may be their significance for the induction of mutation and the origin of melanism in Lepidoptera.

The species used in these experiments were Selenia bilunaria, Tephrosia bistortata and T. crepuscularia, all Geometridae. Of these, no melanic form of S. bilunaria has ever been taken wild; melanic forms of T. bistortata have been reported from Wales, but not from England or Scotland; of T. crepuscularia, melanic forms are prevalent in many industrial areas in England and Wales and on the Continent, but not in the district (South Northumberland and North Durham) where this work was done. In the two first named, the melanism, when it occurs, is recessive; in the last, dominant. The authors have, in all cases, taken care to insure that recessive melanism was not present in the stock with which they started.

The experiments were of two general types. In some, the larvae of the experimental insects were fed on hawthorn gathered by the roadside in an industrial district where melanism is prevalent in many species of moths; while the controls were fed on hawthorn taken from isolated trees growing in a large oak wood, where melanic forms are absent or rare. In other experiments, the experimental larvae were fed on cut twigs of hawthorn placed in 0.1 per cent. solutions of lead nitrate or manganous sulfate (substances stated to be of frequent occurrence in or on contaminated foliage); the controls as before. It was determined that the lead could be found in the upper portion of these twigs in about twenty-four hours, and the food was always treated for this period before use in the experiments.

Experiments of this latter type, on Selenia bilunaria, are the most extensive and critical of those here reported. The essential results are shown in the accompanying diagram (constructed from the text and tables of Harrison and Garrett). Additional crosses in this series, not included in the diagram, serve merely to demonstrate further that the black acts as a simple Mendelian recessive and that it is the same gene in the lead and the manganese experiments.

There are three questions to be answered here: (1) Has mutation occurred in the course of the experiments? (2) if so, has the experimental treatment anything to do with it? (3) where and when, in the germ cell cycle or individual development, has it occurred?



EXPERIMENTS ON SELENIA BILUNARIA

T = type form; b = black form; m = "melanochroic," *i.e.*, intermediate (presumably heterozygous) form. Pb = larvae fed on twigs treated with $Pb(NO_3)_2$; Mn = larvae fed on twigs treated with $MnSO_4$; all others on "pure" leaves. All matings brother-sister single pair, except as indicated.

(1) The only alternative is to suppose that one parent of each of the two batches of eggs with which the experimental treatment began was heterozygous for the recessive black factor, present in the original stock. The absence of blacks in the "controls" by no means excludes this possibility, as the heterozygous forms might easily have been eliminated, by chance, in selecting the parents for the next generation. A much stronger argument is the ratios in which the blacks appear, 26 : 1 and 29 : 2, which depart widely from the 3 : 1 ratio expected on this hypothesis. It is to be noted that the Mendelian ratios in subsequent generations are very good; surprisingly so, in fact, in view of the apparently large mortality and often aberrant sex ratios. The ratio in the manganese experiment, 12 "melanochroic" (presumably heterozygous) : 8 black, is also difficult to explain on the basis of recessive melanism in the original stock. Further, the absence of any previously reported melanic individuals in this species, which is common and widely collected, argues against recessive melanism in the stock. We may, therefore, conclude that it seems highly probable that mutation to a recessive black gene has occurred in the experimental insects.

(2) If this be so, such a mutation must have occurred at least twice independently in the experimental insects (*i.e.*, in the lead and the manganese experiments) and never in the controls or, so far as known, in any other individuals of this species. More-

over, the same kind of thing has occurred in four other cases, in this and the other two species, always in the treated insects, never in the numerous controls. If, therefore, we reject the hypothesis that the melanic gene was present in the stock from the beginning, which is even less probable in the other experiments, we are practically forced to the conclusion that the experimental treatment of the larvae, in some way, whether directly or indirectly, induced these mutations, or at least significantly increased the frequency of mutation in this direction. This does not, of course, prove that the effect is due to a direct action of the lead or the manganese; it might, for instance, be due to some effect of these substances, or impurities in them, on the food plants, secondarily affecting the insects. The most we are justified in saying is that the changed conditions increase the rate of mutation in this direction. There is no clear evidence in these experiments, or elsewhere, of the reverse mutation: two doubtful cases, in one brood, may very well, as the authors point out, be due to contamination. Perhaps the most useful way of looking at these results is to say that the changed conditions alter the relative rates of the two opposite changes, normal $\leftrightarrows$ black, in the gene concerned, thus shifting the equilibrium (in the species) in the direction of black. In the absence of any differential effect of natural selection on these two forms, this must eventually result, under these conditions, in the partial or virtually complete (if the reverse mutation practically never occurs) replacement of the original by the black form. Should these results be confirmed and extended, we have here a possibly highly important factor in the mechanism of evolution; *i.e.*, recurring mutation in a given gene in a given direction, under the influence of changed environmental conditions. This, whether with or without the cooperation of natural selection, may be the sufficient cause of the phenomenon under discussion: the rise and spread of melanism in Lepidoptera in industrial districts. If we grant these conclusions, Harrison and Garrett may fairly claim to have solved the problem in which they were primarily interested.

(3) Granting all this, the most essential question, from a genetic viewpoint, remains. The authors' own interpretation is that the mutations occurred in the individuals in which they appeared. This would involve simultaneous and identical mutations in the somatic and germ cells of these individuals; from which the authors seem to think that some support can be drawn for "Lamarckian" factors, though the logic of this conclusion is not at all clear. Disregarding these gratuitous inferences, an

examination of the facts throws very grave doubts on their interpretation. If the mutations are due, in any way, to the treatment of the individuals in which they appeared, then they can not have occurred before the larvae began feeding, when a considerable amount of differentiation has already taken place. This means (in the case of the lead experiments) that the mutation must have occurred in both allelomorphs in all (or most) of the cells, both somatic and germ, of six individuals, but in none (or very few) of the cells of the other seventy-two identically treated larvae in the second and third treated generations, and in none of those of the first treated generation. If the treatment is really the cause of the mutations, this is beyond the widest bounds of probability.

In the manganese experiments, the results, stated in this way, are even more improbable, involving the simultaneous mutation of one, but not the other, of the allelomorphic genes in all (or most) of the cells of twelve individuals, and of both allelomorphs in all (or most) of the cells of the other eight, in the second treated generation, but in none of those of the first treated generation. In all the other experiments reported, the same difficulty arises.

Critical study of the pedigrees, which can be reconstructed in every case, as in the example here illustrated, from the complete and careful data given in the paper, suggests a simple solution of this dilemma. The clew is furnished, I believe, by the fact that in no case do the mutants appear in the first treated generation. All the facts can, I think, be explained on the supposition that the original mutations occurred (in one or both allelomorphs) in one or a few germ cells of all or many individuals of the first treated generation. These, by ordinary Mendelian recombination, would give some homozygous blacks in the second generation. On this hypothesis, a larger number of heterozygous individuals should occur at the same time. This is the crucial point.

The authors state: "We are able, almost perfectly, to distinguish the heterozygous type of S. bilunaria from the homozygous type." In fact, however, they do not so distinguish, either in the text or the tables, except in two cases, in both of which the forms distinguished as heterozygotes are sibs of the mutant blacks. In numerous other cases individuals which are known, from their parentage, breeding results and the genetic formulas given in the tables, to be heterozygous, are spoken of as "types" or "perfectly typical." They also mention some variation in

the color of the "type" form. We can only conclude, from the facts given, that the authors either can not, or at least did not, distinguish between heterozygous and homozygous "types" in most cases; some of the sibs of the mutant blacks may therefore have been heterozygotes. Examining the offspring of those bred: in the second generation of the lead experiments, of the three "types" bred, one was evidently homozygous, while the other two may well have been heterozygous, as the 17 : 3 in the third generation does not differ significantly from a 3 : 1 ratio. Of the three "types" bred from this brood, at least two were homozygous, while only a third of them should be; this is a fairly probable result of random choice.

In the manganese experiments, a larger number of the germ cells (of the first treated generation) may have been affected, or perhaps they were merely affected earlier, giving a larger proportion of homozygous blacks in the second generation. The twelve "melanochroic" individuals may be partly somatic mosaics of "type," heterozygous and homozygous black cells, due to independent mutations in the second treated generation. Of the two individuals of this kind bred, the germ cells of one may have been all heterozygous or partly heterozygous, partly homozygous "type"; of the other, heterozygous or homozygous black. All the facts in the experiments shown in the diagram are perfectly consistent with the supposition that the mutations occurred in only one or a few cells at a time, possibly all in the germ cells of the first treated generations.

The other experiments, in which the same and the other two species were fed on smoke-contaminated foliage, give consistent results. In one case (Selenia bilunaria), two black and five "melanochroic" individuals appeared, with eighty-four "types," in the second treated generation. In the other cases, the mutants appeared singly in the fifth, sixth or seventh treated generations.

Two cases require special mention. In one strain of Tephrosia bistortata, one individual appeared in the seventh generation fed on smoke-contaminated leaves with "the costal area of the right forewing marked with a broad black stripe, but otherwise perfectly typical." This individual was crossed to one of its "type" sibs and the offspring all bred as heterozygotes; the most probable assumption is that all the germ cells of the mosaic individual were homozygous black, those of its sib homozygous "type." None of the other sibs were tested. The mutation here may have occurred in the early stages of this mosaic individual or in the germ track of one of its treated ancestors; the

mosaic condition, in the latter case, being due to some abnormality, such as double fertilization. Both these kinds of occurrences are well known in genetics.

In Tephrosia crepuscularia, one black individual appeared, with twenty-two "types," in the sixth treated generation; it bred as a homozygous dominant black. The absence of any heterozygous sibs makes it very probable that the mutation must have occurred in the very early stages of this individual. In this, as in the above cited case, the mutation, if it occurred in the very early (egg) stages, must have been due to some effect of the treatment of the parents, if the treatment had anything to do with it. In this species, however, "melanic forms are prevalent in many industrial districts in England and Wales, and on the Continent"; it is just possible, therefore, that this individual was introduced by contamination with the food.

In every case, the treatment was continued until one or more mutants appeared, then discontinued (except in the one case indicated in the diagram). In no case was the really essential control experiment performed: namely, to discontinue the treatment after one or more treated generations and rear the offspring of the "type" individuals on "pure" food; and in no case were the "type" sibs of the mutant blacks interbred and their offspring reared on "pure" food. Thus we have no crucial evidence on this all-important question: did the mutations occur in the individuals in which they appeared or in the germ track of their treated parents?

This work of Harrison and Garrett, if confirmed, is the clearest case yet adduced of the experimental induction of mutation, and may throw light on an important factor in the mechanism of evolution. It has, however, no bearing whatever on the question of "Lamarckism," as the authors seem to suppose.

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A GYNANDROMORPH IN DROSOPHILA FUNEBRIS

MANY gynandromorphs or sex mosaics have been recorded in Drosophila melanogaster by Morgan and Bridges and by other workers; they have also been found to occur in D. simulans and one has been recorded in D. virilis. In the discussion of D. funebris in "The Genetics of Drosophila" Morgan, Bridges and Sturtevant state that "non-disjunction and gynandromorphs have both been carefully searched for in funebris, but without success, in spite of the fact that forked is an unusually favorable character for use in detecting such irregularities."

The writer has been breeding funebris in large numbers for the past year and looking for mutations. In a mutant stock (unpublished data) which resembles hairless of melanogaster and which may represent a recurrence of the hairless mutation recorded for funebris in "The Genetics of Drosophila," a not hairless fly was found on July third, in which the left wing was markedly shorter than the right and the external genitalia were quite abnormal. Both male and female external genitalia were present. The ovipositor was found in the normal position, and there were seven abdominal segments as in the normal female. Posterior and dorsal to the ovipositor a complete set of male external genitalia was present, including anal plates, genital arch, claspers and penis. These structures were rotated through ninety degrees as in rotated abdomen of melanogaster. The twisting placed the anal plates to the left and the penis to the right, a rotation in the opposite direction from that occurring in rotated abdomen. The position of the male genitalia seemed to preclude the possibility of the animal copulating as a male. Furthermore, the work on gynandromorphs has shown that in all cases a gynandromorph with male genitalia was sterile, except in those arising from non-disjunctional stocks, probably owing to the XO composition of the male section of the individual. It was thought that the animal might breed as a female, although the presence and position of the male genitalia might prove a mechanical hindrance to copulation. The fly was placed in a small culture vial with three males and subcultured several times but failed to produce eggs or offspring.

DISCUSSION

It is unnecessary to review the several theories which have been advanced in explanation of gynandromorphs. Most of the cases in drosophila seem to be explained best on the hypothesis

that during an early cleavage an X-chromosome in an XX or XXY individual is lost in the equatorial plate or in the cell wall due to the slow division of one of the X-chromosomes. As a result one of the daughter cells contains one X and the other two X's. The portion of the individual developing from the one X cell is male and the part produced by the two X cell is female. The line of demarkation between male and female sections of gynandromorphic drosophila is generally quite distinct and is undoubtedly due to the determinate type of cleavage found in insects. In some of the cases reported the gynandromorphs are bilateral, and this condition is found even in the genitalia, the left half showing structures of one sex and the right half structures of the other sex. Other cases have occurred in which there have been various abnormalities of the genitalia with parts of the organs of both sexes represented.

The case under consideration is, to the writer's knowledge, unique in that the individual possessed a full set of both male and female external genitalia and to that extent might be called a hermaphrodite. The sexual dimorphism as regards size is more marked in funebris than in melanogaster, the males being considerably smaller than the females. The abdomen of the male is shining black, while in the female the abdominal segments are yellowish brown, with a posterior dark brown band. The short left wing was obviously male and the long right wing female. The abdomen was carefully examined, but so far as pigmentation and number of segments was concerned appeared to be entirely female. As no sex-linked mutant characters were present the critical evidence from these was lacking, and it was not possible to determine the sex condition of different regions of the body with absolute accuracy, as has so often been done in melanogaster gynandromorphs. D. funebris does not have sex combs in the male; consequently this character could not be followed as it has been in melanogaster and simulans.

The writer has no adequate explanation of the presence of a full set of male and female external genitalia. It would seem that the elimination of the X-chromosome must have occurred in that cell which was to form the external genitalia at the time when differentiation of the cell was about to take place or that it occurred so early in the differentiation of the tissue that was to form the external genitalia that it allowed for the complete development of both male and female parts. Furthermore, it would seem likely that in this case the elimination of the X took

place relatively late in embryological development in view of the fact that the only other part of the body to show male characters was the left wing; whereas, if the X-chromosome had been dropped out in a very early stage it would seem likely that the sexual dimorphism of funebris would show itself in a twisting of the body toward the smaller male side and in the pigmentation of the abdomen. The occurrence of this individual is another bit of evidence that the phenomena studied so intensively in melanogaster may be found in other species of drosophila if they are sufficiently investigated.

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THE GENETICS OF HEN-FEATHERING IN CHICKENS

THE exact significance of the different feathering found in the two sexes of certain species of birds has been discussed at length since the work of Darwin. The question of the relation of cock-feathering and hen-feathering of the males of some breeds of the domestic chicken to secondary sexual characters in general and to the endocrine function of the testis have also received considerable attention. It has been demonstrated that gonadectomy or the loss of the function of the gonad in both sexes causes a convergence to a non-sexual, capon type of plumage, regardless of whether the males of the particular breed concerned are normally hen-feathered. The recent experiments of Roxas (1926) on cross-transplantation of testes in the hen-feathered Golden Sebright and cock-feathered Brown Leghorn breeds casts a new light on the situation. They indicate an absence of specificity in the endocrine activity of the testes of the two breeds for the produc-

tion or inhibition of hen-feathering in the males. In other words, one chicken testis appears to be as capable as another of inducing (or inhibiting) hen-feathering. The other genetic factors underlying the development of the character therefore gain weight.

At least two experiments have been reported on the inheritance of hen-feathering. Morgan (1919, 1920) made reciprocal crosses between Golden Sebright bantams (hen-feathered) and Black Red Game bantams (cock-feathered). He concluded that a hen-feathered breed differs from a cock-feathered by the possession of one dominant, autosomal factor. Punnett and the late P. G. Bailey (1921) crossed Silver Sebright bantam hens with a Golden Pencilled Hamburg cock, and later mated birds heterozygous for hen-feathering with those homozygous for cock-feathering. Their results led them to draw conclusions which are in essential agreement with those of Morgan. In both experiments, intermediate males, difficult of classification, were recorded. Morgan included such birds with the cock-feathered, which produced a ratio of 29 hen-feathered to 26 cock-feathered males in the 127 F_2 offspring. Punnett and Bailey classified them as hen-feathered, and thus obtained a back-cross ratio of 229 hen-feathered to 234 cock-feathered males.

It is hoped that certain observations made by the writer on his flock of Golden Sebright bantams may contribute to a knowledge of the genetics of hen-feathering. The flock, which included about two hundred adult birds, during the period of 1914–1917, was maintained for exhibition purposes. The fact that the Golden Sebright bantam is a typically hen-feathered breed has been sufficiently emphasized in the literature. The behavior of the character within the arbitrary confines of such a breed is perhaps of value.

My Golden Sebrights were from two distinct strains which differed markedly in feather shape and length and color of feathers as well as in other characters. By selection, both strains could be made to contribute "standard" birds in each generation, however. In Strain A, the average bird had very short feathers which were laced rather heavily. The black edging also tended to be crescentic, that is, broader at the tip of the feather than at the sides. There were no indications of tail-coverts extending beyond the main feathers. Most of the males, however, possessed feathers on the back, wing-bows and saddle which showed a tendency toward pointedness. The pointed feathers were usually devoid of barbules near the tip. In the darkest

(most heavily laced) feathers the areas lacking barbules were black, but such areas in more lightly colored ones included a yellow edging around the black lacing. Birds of Strain B possessed greater length of feather, and in contrast with Strain A were lightly and evenly laced. The average bird appeared lighter and yellower as a result. The males showed a marked tendency toward the development of long tail-coverts. In most cases the median pair only was involved, while in others the tail became fairly well furnished. The condition became more pronounced with increased age. The feathers of both males and females of Strain B were fully rounded at the tip in all regions of the body (the head and hackle excepted).

Those birds which were the result of a cross between the two strains showed generally an intermediate condition of the characters in which the strains differed to a noticeable extent. The variation among such birds as among members of the pure strains was marked. The variation among the individuals of the two generations following the cross was even more marked. Among the males of the F_2 and F_3 generations were individuals which deviated very considerably from a truly hen-feathered type. The length of feather of Strain B greatly accentuated the resemblance between the pointed feathers of Strain A which lacked barbules at the tip, and true cock feathers. The combination of such pointed feathers with long tail-coverts in a bird caused him to approach very closely in appearance a cock-feathered type.

Remarks on one particular male are perhaps worthwhile. In the late summer of 1916 I found among the young stock of the flock which had been the source of Strain A an unusually richly colored male of about ten weeks. Since most of my birds were somewhat light in ground color and laced too heavily, I bought this bird. He represented a decided deviation in color from the flock in which he was found and from my flock as well. When adult his feathers were of a deep yellow color devoid of lacing in all regions of the body except the breast and thighs. His feathers were considerably more pointed and lacked barbules over greater areas than did those of any other birds of Strain A which I had observed. His tail-coverts were not unusually long. He was mated to several hens of Strain A in 1917, but his chicks failed to show the desired influence of his deep color. They were quite typical members of the strain.

The results which I obtained with the Golden Sebright Bantams when combined with the published results of the crosses of

Morgan, *loc. cit.*, and Punnett and Bailey, *loc. cit.*, suggest certain conclusions. The richly colored male referred to above probably represented a segregation of the recessive allelomorph of hen-feathering. This conclusion is based on three points; namely, his resemblance to castrated Sebrights in color and shape of feather (but not in length of feather), his deviation from the type of Strain A in those plumage characters (except length of feather) in which a castrated Sebright differs from his normal brothers, and the failure of his offspring to show evidence of having inherited his peculiarities of color and feather shape. An analysis of the other males is facilitated by comparing them to this male. It is obvious that they were not in the same class. The principal factor for hen-feathering appears to have been present in both Strain A and Strain B, but its effects on the plumage were partially masked by different sets of factors. Strain A was a highly selected group as regards shortness of feathers, but not strictly hen-feathered. Strain B was a long-feathered group, and in the strict sense more truly hen-feathered. The crossing of the two strains produced individuals having the atypical hen-feathered character with considerably more length than usual in Sebright bantams. It is suggested that these aberrant individuals correspond in certain essential respects to the intermediate males reported in the investigations cited above.

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COUNTED GRAIN POLLINATIONS IN MIRABILIS JALAPA, L.

THE following statement appears in Darwin's "Animals and Plants under Domestication" (Vol. 2, p. 364, first edition, 1868):

> The pollen grains of Mirabilis are extraordinarily large, and the ovarium contains only a single ovule; and these circumstances led Naudin (Nouvelles Archives du Museum, Tom. i, p. 27) to make the following interesting experiments: a flower was fertilized by three grains and succeeded perfectly; twelve flowers were fertilized by two grains, and seventeen flowers by a single grain, and of these one flower alone in each lot perfected its seed; and it deserves especial notice that the plants produced by these two seeds never attained their proper dimensions, and bore flowers of remarkably small size. From these facts we clearly see that the quantity of the peculiar formative matter which is contained within the spermatozoa and pollen grains is an all-important element in the act of fertilization, not only in the full development of the seed, but in the vigor of the plant produced from such seed.

If Naudin's results were confirmed, a clear indication would be given that the size of plants and plant organs is conditioned by factors other than the genetic ones provided for by the chromosome hypothesis. That is—the size of the plants would be determined not only by the reaction of a given gene complex with its environment, but also by accessory material arising from the distintegration of superfluous male nuclei.

It therefore seemed important to us to repeat Naudin's experiment with Mirabilis on a more extensive scale. Altogether one hundred and sixty-one flowers were pollinated, using a single pollen grain in each case. Of these, twenty-three produced normal seeds, resulting in seven plants, which, contrary to Naudin's experience, were quite comparable to the parents in size and vigor, bearing normal flowers and seeds. The corolla spread of the female parent compared with two of the single grain daughter plants is given below:

	Corolla spread in mm									
	23	24	25	26	27	28	29	30	31	Mean
♀ parent	3	1	4	2	2	5	4	1	1	26.7
Single grain, plant A	3	3	7	3	3	4				25.5
Single grain, plant B			1	4	6	8	3	3		27.7

There is clearly no appreciable difference in flower size between the female parent and its single grain offspring. The male parent was not measured, but it was apparently about the same as

the female, since both came out of the same stock. Some measurements were also made of seed weight, since this would probably be different if the single grain plants were weaker. The seeds of the female parent had an average weight of 0.09 gm, the values for the two daughter plants being both 0.07 gm. The number of seeds weighed was fifty in each case. The difference found can not be regarded as significant, as it is less than is usually found between sister plants of a pure line.

To sum up: we find that plants resulting from single grain pollinations are in no way abnormal and are thus unable to confirm Naudin's results.

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